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SCIENTIFIC MEMOIRS,

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NATURAL HISTORY.

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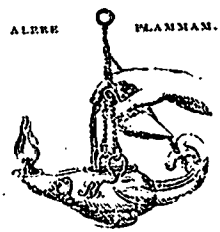
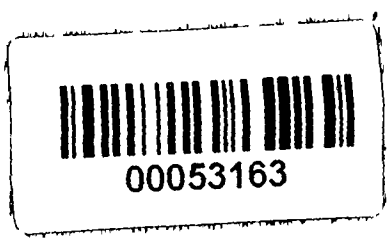


"Every translator ought to regard himself as a broker in the great intellectual traffic of the world, and to consider it his business to promote the barter of the produce of mind. For, whatever people may say of the inadequacy of translation, it is, and must ever be, one of the most important and meritorious occupations in the great commerce of the human race."—Goethe, *Kunst und Alterthum*.



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TWELVE PLATES.

SCIENTIFIC MEMOIRS.

NATURAL HISTORY.

Article I.

On the Circulation of Sap in Plants.
By Dr. Hermann Hoffmann.

[From the *Botanische Zeitung*, vol. vi. p. 377, 1848; vol. viii. p. 17 *et seq.* 1850.]

As, in animal physiology, many of the commonest vital phænomena were involved in obscurity previous to Harvey's great discovery of the circulation of the blood, so in the physiology of plants, not a few points are still inexplicable on account of our very meagre acquaintance with the nature of the circulation of the saps in vegetables.

Every Manual of Botany gives a different view as to the anatomical system in which the saps are supposed to ascend or descend: many deny altogether the descent of the fluids, while others are so firmly convinced of the existence of this, that they have made it the basis of a peculiar kind of descending growth of roots, and stated that trees grow from above downwards, instead of upwards from below. We are likewise ignorant of the relations of the milk-sap to the other juices and to crude nutrient saps, so that it is still undecided whether it is to be

regarded as a secretion, or as a circulating nutrient fluid analogous to blood. Even the function of the air-vessels is not clearly made out, or, otherwise, the recent statement, that the "so-called air-vessels" of the Ferns do not convey air, could not have been made. Under such circumstances, it can only be expected that the imperfect knowledge of the actual facts must leave the *cause* of the movement of the sap in utter uncertainty; and, indeed, on this very point the most wonderful notions are current, capillarity, contractility, and endosmose have to do duty in turn, as far as they will go.

Where is the crude nutrient sap elaborated? How does it arrive there? By what path is it carried back to the other parts of the plant to furnish the material for development? In what anatomical and physiological relation do the air-vessels stand to the system in which the saps circulate?

Injections cannot be applied in the endeavour to trace the paths by which fluids penetrate the vegetable tissues, on account of the minute size of the vessels, nor, indeed, without destruction of the substance. But the spontaneous absorption of easily detected fluids accomplishes in plants what is done by injection in human anatomy. Coloured fluids, however, are rarely taken up by uninjured roots; I have therefore made use of a very dilute solution of ferrocyanide of potassium, which may be readily detected in any spot to which it has penetrated, by the blue colour it assumes when chloride of iron is applied. And as the Prussian blue thus formed is insoluble in aqueous fluids, a little care in slicing and preparing the objects enables us to avoid the spreading of the colour to unaffected parts, which would deceive the observer as to the boundaries within which the natural motion of the sap takes place.

In the first place, it is found that this fluid penetrates by a different path in uninjured roots, from that which it takes when the solution is caused to be absorbed directly by the cut surface of a cut plant; in the next place, that the course which this fluid pursues is constantly the same, and peculiar to each plant; and, moreover, that by no means all cells and vessels take equal share therein, but that where, in general, vessels are met with, the sap enters first into these, and then, as in animals, passes far more slowly from these into all the remaining tissues of the plant.

By this means it is possible to test, by direct experiment, the directions and course of the flowing saps from the root to the leaves, and backwards to all the other organs, which the following observations attempt to do in regard to the more important families of plants.

I. Acotyledons.

1. *Fungi.*

Clavaria rugosa, Bull.—A number of these fungi (with uninjured radical filaments imbedded in earth) were placed with the lowest part in an aqueous solution of ferrocyanide of potassium: in twenty-four hours they had become thoroughly imbued with it, so that a blue colour was produced when the tips were merely slightly touched with chloride of iron.

When a cross section of the upper part of the fungus was made, and the surface of this tested, a blue colour was also produced, but of very different intensity in different parts of the section. One part remained almost white, while the central portion, as well as a zone within the layer of rind, was strongly coloured: the hymenial layer was tinged but very slightly, which appears to depend partly on the great density of the cellular tissue, offering more resistance to the passage of the juices, and partly on the similar effect of the horizontal position of its cells. The cells of the interior were of perfectly similar character, but they seemed to be more loosely packed under the cortical layer and in the central part, and the more active conduction of the fluid is connected with this. The walls of the cells, and also the fluid between them, were coloured blue. Longitudinal sections exhibited exactly the same results.

Scaphophorum agaricoides, Ehrb.—The little branch to which the fungus was attached was dipped into the fluid, without wetting the fungus itself. In twenty-four hours the fluid had made its way to about the middle of the fungus; when chloride of iron was dropped on the surface, a blue colour was produced, and this arrested the further penetration of the ferrocyanide of potassium toward the border, so that the latter did not exhibit any reaction even after two days.

Although this fungus is composed of uniform elementary structures, the reaction of the different layers displayed very

unequal intensity; for while the sections of the lamellæ were still white, an intense blue was shown in the angles of their folds; the fleshy substance in the vicinity was likewise white, while the same exhibited two strongly coloured layers farther up; the superficial layer was also coloured deep blue. Microscopical examination shewed that the lower part of the cellular tissue which had remained white was more closely packed, with predominant transverse joints, whence the fluid could not pass so readily; while the upper part, distinguished by its deep colour, facilitated the penetration by the laxity and the varied direction of its cells.

Trametes suaveolens, Fries.—Several drops of the test fluid were poured upon the bark of the willow stem upon which the fungus grew, near the point of attachment, but without wetting the plant itself. In two days the fungus exhibited a tinge of blue, chiefly at the places where it was attached to the slice of bark, and consequently it must itself have contained a salt of the oxide of iron; this slight blue colour was also visible on the outside of uninjured fungi. On the application of chloride of iron to the surface of perpendicular sections, the colour became deeper near the base, and spread somewhat farther, especially in one point as far as the hymenial layer.

Agaricus virgineus, Pers.—The patch of turf on which it grew was placed in the fluid, and within three hours the entire fungus was penetrated by the latter, which is not wonderful considering the great moisture of the plant. Stipe, pileus, flesh, and gills, were coloured deep blue in the reaction, the pileus darkest at the part where it is continuous with the hollow stipe, while the sections of the gills were only weakly tinged, or did not become coloured at all; but the passage of the blue-coloured into the uncoloured parts was quite gradual, and exhibited no distinctly marked boundaries. Examination by the microscope revealed a very lax interwoven cellular tissue; in the lighter spots, cells were seen only half coloured blue, so that the fluid had not completely penetrated them.

From the foregoing it appears that the path of the circulation has no accurately fixed boundaries in the Fungi, and presents no anatomical peculiarities; the fluid penetrates forwards and laterally between and in the cells, proceeding most rapidly in those

places where the laxity of the tissue and the direction of the cells oppose the smallest amount of resistance; just as in blotting or other unsized paper.

2. *Lichens.*

Cladonia subulata, Wallr.—The lumps of earth on which the plant grew were placed in the test fluid, and the whole was covered with a plate of glass, in order to maintain a moist atmosphere. Yet even after ten days the plant was not permeated throughout; it had become coloured blue in some places, which indicated a natural existence of salts of oxide of iron in it. After the application of chloride of iron, moreover, to various sections, only a slightly deeper blue colour presented itself, which is readily explained by the extraordinary density of the tissue, and the consequent slow conduction of the juices in the lichen, which is itself of a rather dry nature. The blue colouring was uniform, and exhibited no marked limits.

3. *Mosses.*

Syntrichia ruralis.—The moss and the soil supporting it were so placed in the fluid that the former remained unwetted; the atmosphere was kept damp as above. The stem conveyed the fluid upwards; the leaves exhibited an uniform blue colouring at the base, which however spread very slowly over the surface, when the chloride of iron was dropped upon them; the fluid advanced much more rapidly towards the point in a row of cells lying close beside the margin, while the mid-nerve acquired no perceptible colour. The chlorophyll granules did not seem to exert any especial influence on this conduction, since the lowest cells appeared coloured uniformly blue, in spite of their total absence. In the cells lying somewhat higher up, the blue colour did indeed correspond with the heaps of chlorophyll, which was perhaps only an optical phænomenon: further up the cells were pure green.

Barbula muralis, Timm.—Treated as above: half mature, like the foregoing. Here again a blue stripe of more delicate cells was seen along the margin up to the apex, after the application of the reagent, while no discoloration could be detected in the mid-nerve, and on the general surface of the parenchyma of the leaf only isolated spots occurred, appearing to indicate a very

imperfect conduction of the sap in these places. The fruit-stalk absorbed only a small portion of the fluid extremely slowly; when cut across, and the cut surface dipped in the solution of ferrocyanide of potassium, it soon exhibited a very distinct reaction; strongest below, where rind and pith were coloured; weaker above, where only the pith was acted on (and this slightly).

From this it appears that the passage of the sap goes on chiefly and most energetically in a peculiar layer of cells along the margins of the leaves, in these mosses, while the mid-nerve fulfils another function; I could not detect air in the latter. The stem and the fruit-stalk conveyed fluid onward through all their tissues, but very slowly so long as they remained uninjured. When chloride of iron was applied to the uninjured rind, it penetrated extremely slowly, which is sufficiently explained by the solidity of the structure.

Hypnum cupressiforme, L.—In this there are no peculiarly-formed marginal cells and no mid-nerve; and no definite direction of the course of the sap could be detected here. This plant became gradually saturated with the fluid, so that even the peristome was coloured blue.

4. *Ferns.*

Pteris serrulata.—The test fluid was dropped upon the mould in which the plant was rooted, without wetting or injuring the latter. In twenty-four hours it had already penetrated far up the petiole; the reagent did not colour the brown internal layer or the vascular bundle in the central point; the latter was white, surrounded by brown soft cells. The parenchyma was blue and rich in granules (chlorophyll and starch?) throughout. The scalariform vessels in the interior distinctly contained air, and when uninjured took up no test fluid, although the plant was in a most vigorous condition of growth.

Polypodium crassifolium.—Treated like the preceding. In twenty-four hours the petiole was permeated by the fluid, and both the rather delicate cortical layer (of a green colour), containing no chlorophyll, and the entire parenchyma, which contained very numerous granules, were coloured blue by the reagent. The latter is traversed in the inner parts by isolated vascular

bundles which are surrounded and supported by a hard brown layer of cells of a glass-like brittleness. These were not coloured blue; neither were the vessels in their centre, which evidently contained air, and were to a slight extent unrollable. When this petiole was cut across and the open end dipped in the test fluid, the latter penetrated very rapidly upward into the white air-vessels, driving out the air. If the upper part of the leaf was dipped in the fluid, the phænomena were the same as in the first case; under such circumstances nothing penetrated into the air-vessels, which consequently are nowhere in communication with the surface (the stomates).

Aspidium capense.—The phænomena were exactly the same as in the preceding instance. Here again the stomates on the under side of the leaf conveyed no fluid into the air-vessels in the interior.

Aspidium filix mas, Sw.—The results did not differ from the foregoing. The brown cells again were not coloured blue here. Hence the Ferns possess distinctly separate paths for the diffusion of air and sap. I could not observe any special path for the descending juices, and the existence of such may indeed be doubted, since these plants are supposed to grow only at the points.

II. Monocotyledons.

In the preceding section an attempt was made to prove that in the lower cellular plants, in accordance with their homogeneous structure, the fluids passing from the soil into the plants, took no fixed direction, but, soaking through from cell to cell, advanced most rapidly wherever the laxity of the tissue opposed the minimum of resistance. In the Vascular Cryptogams, on the contrary, in the Ferns, it was found that special organs, the streaked vessels, already present themselves, exclusively destined to contain gaseous fluids, while the fluids absorbed from the earth first ascended within the looser *cellular* tissue in the vicinity of those vessels, and were from thence diffused throughout the remainder of the tissues of the vegetable; not indeed without previously undergoing suitable elaboration and amelioration.

In the Monocotyledonous plants, where the specialization of the anatomical systems becomes more distinctly marked, similar

results are met with, and it is especially seen here, that the function ordinarily attributed to the system of the spiral vessels and their allies, is devoid of all proof in fact, and has been deduced from experiments in which sufficient regard was not paid to all the circumstances involved. At the conclusion of the third part of this essay, relating to the Dicotyledons, I shall examine these experiments more closely, and seek to demonstrate the causes which have so long restricted us to conjectures and opinions, in a matter which appears so simple.

Since in the plants now to be considered, new organs, flowers, organs of fructification, and ovules, are added to those already examined; since, moreover, a far greater variety becomes evident in the forms of the internal structure, and the physiological relations of the roots, stem, leaves, &c., of the Monocotyledons, than exists in the majority of the Acotyledons; the observation of the progress of the sap within these different structures, possessing peculiar forms in the diverse families, acquires greater importance, and admits of conclusions of a far more comprehensive nature. I therefore take permission to enter more minutely into the details, in order to introduce the more extended remarks in fitting places.

The experiments, as in the above-mentioned cases, were made, with the exception of *Canna*, on pot plants alone, which were treated in the ordinary manner. In order to discover the course of the sap, the earth was watered with a solution (always of pretty equal concentration) of ferrocyanide of potassium, and then, after this fluid had been absorbed by the uninjured roots, the parts where absorption had occurred were demonstrated in transverse and longitudinal sections of the plants, by means of sulphate of peroxide of iron.

Anomatheca cruenta, Lindl. (Iridaceæ).—Watered on the 16th of July; in two hours the ferrocyanide of potassium could be detected in the bulbs, while it was sought in vain in the stems. In the petals also (even in those developed subsequently to the watering and investigated three weeks after), the sap could not be traced, although at first appearance it seemed to have entered them, since they contain a red colouring matter which is readily decomposed and changed into a *blue* colour; but a counter-experiment with *pure* water, with a careful application of the

reagent to the petals (stripped of some of the epidermis by shaving with a razor), showed the error of the first conjecture. Into the sepals of the specimen, on the contrary, the sap ascended within a few days; the same occurred in some half-ripe fruits which existed upon other specimens. The following is a detailed account of the anatomical conditions.

The bulb does not consist of separate scales, but forms a kind of tuber which is chiefly composed of a perfectly homogeneous mass abounding in starch; the outer coat is a reticulated shell composed of two membranes: a thick bundle of vascular cords runs up the centre. The starchy parenchyma does not react blue, neither does the vascular mass in the centre, in the separate vessels of which air may be detected by the microscope; but a very dark blue colour was seen in innumerable closely-crowded little points in the cortical layer or shell. And the presence of the ferrocyanide in the cortical substance did not depend upon a penetration from without during the watering of the specimen, and thus upon a penetration into the interior by an unusual path; for the outer coating of all showed no reaction whatever with the salt of iron, while the blue colour was scarcely perceptible inside the finest of the root-fibrils. The shell of the bulb contains no air-vessels or spiral structures, but is traversed in all directions by numerous anastomosing liber bundles, which are sharply defined against the looser cellular substance surrounding them, and give the shell the open reticulated aspect already mentioned. These liber bundles exhibited no reaction; in the transverse section they look like large yellowish circles, which are clearly contrasted against the surrounding blue cellular spots. The cells lying between these bundles are of two kinds; those lying next them are narrower, more slender and more elongated than the rest, which exhibit a rounded four- or five-angled form; it was these *elongated cells* which were coloured *blue* by the application of the salt of iron, while the remaining cells remained for the most part altogether uncoloured. The blue-coloured cells frequently lie several one behind the other, so that it is easy to trace the straight line in which the sap advances, without deviating to the side; in other cases, especially in the rest of the parenchyma, they frequently lie isolated, whence it appears to follow, that the motion of the sap is not

only less perfect in general here, but also takes place in an irregular manner, by no means in one and the same plane (parallel to the surface of the section). This tuberous bulb is, evidently, remarkably well fitted to afford a clear notion of the organs conveying the sap in plants, since here all the important parts, the spiroids, the parenchyma, the elongated vessels, and the liber, are distinctly, and in fact—as in the Dicotyledons—widely separated from each other, to the great convenience of the observer.

Underneath the bulb is the true root, which is of a pointed conical form. Here also the vascular bundles lie in the middle, while the blue colouring occurred in the parts more toward the circumference. In the stem no discoloration could be perceived, even in the cases where distinct reaction occurred, not only in the bulb below, but also in the capsule at the upper end. From this it seems as if the absorbed sap rested or became accumulated in particular parts of the plant, while it only hurried through the others as passages. In the cases where reaction was observed in the calyx, microscopical examination showed that the air-carrying, delicate unrollable spiral vessels or annular vessels were never the organs conveying the sap, but the elongated cells often lying close beside them. In specimens which were taken up nine days after watering, the absorbed ferrocyanide could be detected inside the half-ripe, otherwise fully-developed, capsules. It occurred within the elongated cells, which always accompanied the numerous delicate air-vessels in the axis, and seen through a lens after the reaction, formed a great abundance of little blue points and streaks. The soft, unripe seeds also exhibited distinct reaction in particular places; here the fluid had also been conveyed from cell to cell through the seeds; no vessels of any kind exist in the seeds.

Tigridia pavonia, Pers. (Iridaceæ).—The plant was watered with the ferrocyanide while in full vegetation, on the 25th of July. After six days the reaction was observable not only in the bulb but also throughout the whole stem up to the floral organs, but not in these or in the interior of the germen. In nine days, however, the germen also had absorbed the salt, close beneath the surface, but neither the interior nor the ovules exhibited any reaction. The current had advanced more externally to the upper parts, to supply the floral organs with sap in the first

instance, since a strong influx of sap and an active vegetation do not exist in the ovary and the ovules until they are fully developed. In the flower-bud of a blossom unfolded on the same day, the reaction could be detected in the petals, the stamens and in the pistil up to the stigma.—The root: this is placed underneath the bulb, and is of a swollen conical form. Internally it is homogeneous, and in the centre is found the bundle of striped vessels; the blue colour was seen to a slight extent surrounding this, but much more marked at the peripherical layer.—Bulb: it consists of the bases of some six stems, enveloped by the sheaths at the bases of leaves; the vascular bundles are scattered irregularly in the former; no reaction could be detected in the bases of the stems. Inside the bulb-scales the vascular bundles lie at some distance from each other in the median layer, while the reaction brought out a great number of blue spots, both in the *mesophyllum* and, more especially, beneath the inner and outer epidermis of the bulb-scales. In the outermost coats of the bulb the blue colour was not limited to isolated points, but diffused uniformly throughout the entire *mesophyllum*, with the exception of the vessels. Microscopical examination of longitudinal sections showed that the vessels contained air and were uncoloured, while the cellular tissue and especially a portion of the elongated laxer cells were coloured deep blue. It is remarkable that only a portion and not the whole of the elongated vessels were concerned in the first conveyance of the sap. In longitudinal sections it was seen that these cells were much more easily separated from each other laterally than at their ends, by pressure, which seems not unimportant in reference to the conveyance of the sap.—Stem: in a cross section half-way between two nodes, the reaction made visible a large number of blue points, both inside the cortical layer and in the layers of the central parenchyma. The cortical layer is composed of few, narrow, striped vessels, liber bundles with very long cells colourless as glass, and of elongated cells which were in part coloured blue; the layer allied to liber found at the circumference of the central parenchymatous substance of the stem, which is very thick in the internodes, while it is far weaker at the nodes, did not become coloured. The vascular bundles are scattered in the internal substance and were not

coloured; they are connected with the compact parenchymatous cellular tissue by a lax tissue of delicate prosenchymatous cells, forming an investment around them. When the preparation was dried these were partially torn away, and the vascular bundles hung loose in the tubular cavities thus produced. In longitudinal sections the vascular bundles were seen most distinctly of a yellowish colour; between and beside these the blue streaks and points which indicated the sap-bearing cellular tissue. —Flower: when the epidermis had been removed it was easy to detect the reaction here also, and it was seen uniformly throughout the parenchyma (containing colouring matter) of the petals, while the vessels and the delicate parenchymatous cells accompanying them remained free. The stamens, conjoined into a tube, in the angles of which two vascular bundles are found, exhibited blue points both at their inner and outer boundaries, while the style lying free in the tube of the filaments was only spotted with blue in its outer periphery. The stigma was found very uniformly permeated with the salt.

Dioscorea bulbifera, L. (Dioscoreaceæ).—Within seven days after the watering the salt had already ascended five feet up in the stem.—Root: upon reacting on a longitudinal section the whole tuber was found spotted with blue points and streaks; no colouring occurred in the yellowish-white pieces of vascular bundles, which, composed of striped vessels containing air, were visible here and there, nor in a considerable number of reddish spots which microscopic examination proved to depend upon large drops of yellowish red oil occurring in many of the cells. The blue was seen inside the parenchyma of which the tuber is almost exclusively formed, in the same cells which contained starch. In a cross section of the Stem are seen a number of small and also very large vessels not combined into bundles. The larger are in many places situated at pretty regular distances, forming something like a hexagonal figure in the parenchyma of the stem, while the small are scattered quite irregularly, and often enveloped in a pretty thick coat of elongated cells. Inside the central parenchyma or pith occurred isolated blue points; the broad woody layer on the contrary was wholly devoid both of these and also of vessels, while by far the greatest mass of the salt had ascended in the elongated cells of the liber and

cortical layers, and had become more or less diffused from thence into the surrounding parenchyma of the rind. The large vessels of the stem just mentioned are of so great diameter that a hair may be easily passed more than an inch down them. When the stem was cut up, some of the fluid almost always escaped from the wounded sap-bearing cells of the circumference and penetrated into the interior, as also in the garden balsam, where the size and transparency of the tracheæ invite such experiments, giving an appearance as if these canals were not really air-vessels but sap-conduits. Disregarding the fact that, in my experiments, their walls and their rather fluid contents never exhibited a blue colour, the original presence of air in them may be easily directly demonstrated. For if a stem held the wrong end upwards is cut across and the wound immediately dipped in a drop of thick solution of gum, there is no difficulty in seeing bubbles of air emerge slowly from these tubes and inflate the dense fluid, when the stem is squeezed from the root upwards toward the wound. The ascent of bubbles of air begins directly, even when the pressure is commenced six inches below the wound, and it continues without interruption if the pressure is advanced slowly upwards to the cut surface. To conclude from the wholly accidental presence of water in these tubes, that they are normally conductors of liquid, is like deducing from the presence of blood in the air-passages of a decapitated animal, that the lungs are naturally intended for that fluid. While the smaller vessels of the stem are usually spiral vessels, the structure of the larger is very well worthy of notice, for their walls look as if formed of small, nearly quadrangular frameworks, over which a delicate, closely spotted membrane appears stretched. The petiole, like the stem, is very rich in starch-bearing parenchyma; it is coated by a rind, the partly elongated cells of which (but not the liber cells) become deep blue; the internal tissue exhibited very few blue points, and the isolated spiral vessel bundles, in which air was clearly seen under the microscope, bore no share in the colouring.

Rhapis flabelliformis, Ait. (Palmaceæ).—The plant, a specimen three feet high, was penetrated throughout all parts by the fluid in ten days after watering.—Stem: a transverse section, at least in the upper part of the plant, displayed this enclosed in the

sheath of a leaf (like the scale of a bulb), which was especially rich in sap and reacted strongly, while at the lower part of the stem this part was already dead and in a great measure decayed away. In this sheathing base of a leaf the elongated cells had chiefly absorbed the salt, while the liber bundles were not discoloured. The principal mass of the vessels (their walls present short streaks) lie in some degree concentrically, at equal distances from the centre and the circumference; the vascular bundles, with their woody envelopes, contained air and were not discoloured; but in the rounded, four-sided, starchy parenchyma cells between them, blue points were observed, which occurred in proportionately largest quantity in the vicinity of the central point and of the periphery. In a longitudinal section it was seen that the reacting cells exhibited scattered points or little streaks, and never lines continued in one plane. The vascular bundles run pretty nearly parallel in the stem; even the nodes exert no influence upon the arrangement of the internal parts lying opposite to them. When the stem was cut through higher up, where it begins to lose itself in the leaves, a different appearance was seen. Yet microscopical examination showed that here again the salt had not ascended inside the vessels, but only in their immediate neighbourhood, inside the elongated cells by which they are accompanied. The upper leafy, as well as the peripherical, parts of this plant reacted far more strongly than the interior of the stem.

Commelina cœlestis, Willd. (Commelineæ).—This plant was watered on the 17th of July; the examination was made on the 24th and 26th of July, and the 9th and 15th of August, but in all cases the salt was sought in vain in the parts of the stem situated between the nodes, while in the nodes themselves, from the lowest to the uppermost, the reaction could be easily detected. From this it appears, taking the other experiments into account, that we must conclude the sap to rest for a time in particular parts of plants, as in tubers, nodes, buds and ovaries, while it hurries rapidly through others, especially the internodes of the stem. The cross section of the nodes of the stem exhibits a distinct separation into pith and rind. The bundles of spiral vessels, which displayed bubbles of air in their interior when examined with the microscope, exist both in the pith and the

cortical layer; in the internodial parts of the stem the cortical layer is contracted further inwards, so that there is not so sharp a line of demarcation there. The points displaying the blue reaction were among isolated roundish cells which occur internally and externally in the neighbourhood of the vascular bundles. In longitudinal sections the blue points appeared in an irregular band passing transversely through the node. In buds examined four weeks after the watering (they had been developed during this period), blue colouring could be detected inside the elongated cells of the calyx and the stigma, and inside the minute parenchymatous cells of the (still white) petals and of the connective, while the delicate spiral vessels, even in the youngest, still imperfect organs, never displayed any colouring. It is worthy of notice that the epidermis of the petals opposes such a resistance to the penetration of the salt of iron, that no reaction occurs even when the entire petal is dipped in sulphate of iron; hence it is necessary to tear the epidermis carefully away to admit the sulphate of iron to the parenchyma when we wish to bring out the reaction.

Commelina pubescens.—The presence of the ferrocyanide could be shown in the cells of the stem and leaves five days after the watering.

Commelina clandestina, Mart.—Here also the absorption could be certainly demonstrated after a short period.

Commelina angustifolia, Michx.—Detected certainly after four days.

Commelina tuberosa.—The absorption demonstrable in two days, both inside longish cells and in isolated large cells of the central parenchyma.

Gladiolus psittacinus, Hook. (Iridaceæ).—Here again it was easy to trace the salt many inches up the stem, and above all in the elongated cells, in which it was very uniformly diffused, and which are in part situated close to the air-bearing spiral and annular vessels, and in part at a distance from these and near the inner and outer epidermis of the separate leafy sheaths, of which the stem is almost entirely composed. The inner and softer leaf-sheaths of the stem reacted most strongly and consequently appeared to convey the sap most actively. These plants must contain a salt of peroxide of iron as a natural constituent,

for in four weeks after the watering, the leaves spontaneously exhibited a deep blue colour at their tips. The plants all died in little more than a month, apparently in consequence of the watering with the ferrocyanide, since they were placed in conditions otherwise favourable.

Tritonia fenestrata, Ker. (Iridaceæ).—Within two days after the watering, the salt could be detected in the bulb and in the lower part of the tuft of leaves. The lower part of the bulbous mass (which is the bulb formed the year before, or real tuber) was coloured very deep blue throughout; in the upper bulb (of the current year) it was observed that the parts giving a blue reaction were little scattered points and streaks, which were universally distributed. The microscope showed that those lying in the central part were the elongated cells which surround the air-bearing vascular bundles; in the parenchymatous part of the tuber the blue colour was deepest in the starch-filled, irregular parenchymatous cells of which this structure is composed. The circumstance that in all cases, and especially distinctly here in the longitudinal section, the blue-coloured cells were mostly scattered and only exceptionally formed uninterruptedly continuous lines, proves that the passage of the sap does not take place uniformly through all parts indifferently, but peculiarly through certain cells, which do not lie all in the same place (parallel to the surface of the sections), but more or less scattered, causing a ramification of the currents of sap often of a very irregular character.

Allium neapolitanum, Cyr. (Liliaceæ).—Not even four weeks after the watering could the presence of the ferrocyanide be detected either in the interior of the bulb or in the stem. On the other hand, the outermost dead scale of the bulb was coloured of an uniform blue tint, evidently by accidental imbibition of the fluid in contact with it, not only in the cells, but both in the reticularly striped and the true unrollable spiral vessels, which, moreover, still here and there displayed air in their interior.

Canna indica (Canneæ).—This plant was growing in the open air and was watered on the 17th of July. In seven days the blue reaction could be readily detected in the stem. This exhibits somewhat the same structure as the Palms in the cross section

(vide *Rhapis flabelliformis* above), except that the vascular bundles of the true axis are very irregularly scattered in the interior, while they are arranged in a tolerably even radial order towards the circumference. In the main axis itself the salt could not be demonstrated with sufficient certainty at this time, but with the greatest ease in the sheath (the base of a leaf) which firmly enveloped the whole main axis. Here the blue points were found in greatest abundance close beneath the outer epidermis, but also in large numbers immediately surrounding the liber bundles (enclosing unrollable spiral vessels). The microscope proved that the blue colour existed exclusively in uncommonly continuously stained cellules (containing large nuclei) arranged in very straight longitudinal rows close beside the vascular bundles. The arrangement of the spiral vessels, liber-bundles and sap-conduits in the leaves was similar to that in the stem.

Panicum plicatum, Lam. (Graminaceæ).—Had not absorbed the least in four weeks; the same happened in *Ruscus aculeatus* and *Ananassa sativa*.

Arum divaricatum, L. (Aroideæ).—These plants had, for the most part, absorbed nothing at all even after four months; in the few cases in which a weak reaction could be detected in the tuber, the blue colour was found in the large parenchymatous cells of the general substance, which contained the unusually thick starch-granules, of beautiful pyramidal and polyhedral forms with rounded faces; while the scattered yellowish bundles of partly round, partly angular annular vessels were never discoloured.

Tradescantia discolor, L'Hérit. (Commelinaceæ).—The reaction was visible in the stem in four days after the watering. The investigation is most difficult in the upper leafy parts, although they are coloured deepest, because immediately the cortical layer is cut across a great quantity of thick gummy liquid exudes, which covers the whole surface of the section and confounds all the previously distinct fluids together. But when the stem is cut lower down, a few inches from the ground, the interior is found far less rich in sap, only a little mucilage exudes, and it is more clearly seen when the absorption of the salt has

occurred. A cross section at this point presents the following appearance. At the outside a cortical layer, without vessels, the starchy parenchyma of which is separated from the large central parenchyma of the stem by a kind of liber-layer: the central parenchyma, forming the great body of the stem, contains scattered vessels divided into two sets, a central and a peripherical, between which lies a ring of parenchyma free from vessels. The cells which became blue lie in the vicinity of the vascular bundles; the gummy cortical layer was devoid of them. It is worthy of notice that both the boundary between the liber and parenchyma, properly the outermost layer of the central cellular mass, and the immediate environs of the vessels scattered in the central mass, emitted a small quantity of a tenacious white sap, in which were suspended a few starch-granules and an extraordinary quantity of minute raphides. No ferrocyanide could be detected in the cortical layer even after the space of a month.

Chlorophytum Sternbergianum, Steudl. (Liliaceæ).—In this plant, which appears to derive the greatest part of the requisite moisture from the atmosphere, it is difficult to diffuse a quantity of the salt sufficient for the reaction in the ordinary way. The slender filiform stem to which the tuft of leaves with their aërial rhizomes and roots is attached, died in a few weeks, in consequence of the watering, without much of the liquid having been absorbed. In this case the cells of the bases of the leaves, as also the aërial roots and the rhizomatous tubers, exhibited a weak blue colour when cut surfaces were wetted with sulphate of peroxide of iron. A clearer view may be obtained in a different way. The aërial roots readily absorb fluids, for instance water, when they are dipped into it; moreover, sulphate of iron was decomposed, the oxide fell as a yellow powder to the bottom of the glass, while the water penetrated into the plant; on the other hand, a large aërial root which was already buried in the earth and had taken root there, readily absorbed so much ferrocyanide that this could be easily detected in longitudinal and transverse sections several inches above the ground. The central layer containing the dotted vascular bundles was found free from colour; but all the rest of the tissue, composed of

elongated cells, even close in the vicinity of the former, had absorbed a considerable quantity of the salt, and exhibited innumerable blue dots and streaks in the longitudinal section.

Caladium viviparum, Roxb. (Aroideæ).—The fluid could be detected in all parts of the tuber and petiole twelve days after the watering. Minute examination showed the root to be a true tuber, which in three weeks after the watering was found softened, collapsed, and, in short, dead (probably in consequence of the watering); on reaction it turned uniformly blue all through, just as a sponge would do under similar circumstances. On this tuber is seated the bulb-like base of the stem, which encloses within it the true terminal bud of the axis. Both the base of the stem and the central bud exhibited distinct reaction in the same way; in longitudinal and cross sections they became covered with countless blue points, which were recognized under the microscope as elongated cells. A leaf-bud which had just been developed from the tuber had likewise absorbed the salt, especially in its central region. The investigation is difficult in the fully developed leaf-stalk, since this so abounds in sap, that the fluid exuding when it is cut across readily spoils the experiment with the reagent. The blue sap is found in the elongated cells which surround the numerous round liber-bundles of the thin peripherical or cortical layer, the latter enclose isolated delicate unrollable spiral vessels*. The whole of the interior of the leaf-stalk is composed of parenchymatous cells, inside which run not only ordinary liber-like cells with vessels, but also several canals, so large that a hair may be readily introduced into them. These canals, still filled with fluid in the bud above mentioned, contain air in the fully developed petiole; when the latter is squeezed even six inches from a cross-cut surface, air-bubbles are forced out of them; just as was described above of the *Dioscorea*. The walls of these air-cavities are composed of large cells; these tubes therefore form a transition to those of *Dioscorea*, which exhibit a great affinity to the ordinary pitted

* The numerous thick-walled raphides-cells occurring here slowly expelled their contents when accidentally injured, and these spread out like a tuft of feathers, displaying a peculiar backward movement not unlike that of the Oscillatoriæ.

wood-vessels. In the interior of the petiole the absorption of the sap was indicated only by a few spots becoming blue.

Aloe picta, D.C. (Liliaceæ).—Not even after five weeks, any more than at several shorter periods, could I detect the slightest trace of the salt in the roots, buds, stem or leaves of these plants, which were perfectly healthy, and which scarcely betrayed any injury even at the point of the main root in consequence of the watering. It is true the application of the salt of iron to a cross section discoloured the yellow fluid (the aloe-bitter) which exuded, transparent, from the large, very much elongated cells near the spiral vessels at the whole periphery of the leaf, but the stain was brownish black, not blue; a reaction which occurred also with Aloes of this species never watered with the ferrocyanide, and which therefore must be attributed to tannic acid. The absence of absorption after the stated period is the less remarkable, since these plants remain for seven months of every year in a dry part of the conservatory, without ever being watered, therefore without requiring any other fluid than that which they receive through evaporation when other plants are watered.

Zephyranthes grandiflora, Lindley (Amaryllidaceæ).—Three days after the watering no reaction could be detected in the bulb, petals, or ovules; four days later, however, the bulbs exhibited distinct blue spots both in their outer and also in their inner scales, but the yellowish vascular bundles were not stained. The different lamellæ of the bulb consist here of two epidermal surfaces, of parenchyma-cells full of starch, of elongated cells which are very soft and loose, and especially contained the blue fluid, and next to these, in the median line, of unrollable spiral and annular vessels, surrounded by a few delicate prosenchymatous cells, as is usual in herbaceous plants. At this period no salt had penetrated into the stem, not even into the lowest part next the bulb. The plants in the same pot all died within eleven days.

Cyperus monandrus, Roth (Cyperaceæ).—Nine days after the watering the ferrocyanide was found in the stem and branches. The rhizome, which was dug up after thirteen days, was, like the whole plant, perfectly stiff and healthy, as was the case with

almost all of the plants mentioned above, so far as the researches here described go to show. The transverse section showed that the salt had perfectly penetrated this, with the exception of the yellowish vascular bundles which run in the thick parenchymatous cylinder; otherwise a great quantity of dark blue cells were found in all parts among the uniformly light blue mass of cells. In the lower parts of the stem the reaction was only weak; it was more distinct in the peripherical part (no rind existed here) further up; it was strongest at the apex, where the separate flowering branches go off, for here not only the periphery but also the interior of the stem was closely sown with blue spots (streaks in the longitudinal section), which under the microscope were seen to be elongated cells: the angular, dotted, and small streaked vessels which were situated partly near the periphery and partly deep in the parenchyma of the stem, contained air and had no share of the colouring.

III. Dicotyledons.

In these plants we meet with a phænomenon which is not observed in those divisions of the vegetable kingdom above investigated, at all events not in Germany, namely, the "bleeding," or "tears," which occur on wounds of many of the shrubs and trees of this division in early spring.

This phænomenon is so peculiar that it will be advantageous to examine it separately. In the following experiments I investigated, 1st, the course of the spring sap; and 2ndly, that of the summer sap, independently.

1. *The Spring Sap.*

1. On the 27th of February 1850, a root A, of $\frac{1}{2}$ an inch diameter, coming from the west side of a white birch 6 inches in diameter, was laid bare, cut across, and the upper cut end placed in a cylindrical glass, of about 1 cubic inch capacity, filled with a solution of ferrocyanide of potassium. This was done at four o'clock in the afternoon. By the next morning the fluid was absorbed as far as the root reached.

On the 27th also, several holes of $1\frac{1}{4}$ line diameter were bored $\frac{1}{2}$ an inch deep, and into these introduced and cemented quills

of the same section, with the inner ends cut off obliquely and the orifice looking upwards. These borings were made,—

B, 3 feet above the ground, on the west side.

C, $3\frac{1}{2}$ feet above the ground, on the south side.

D, 5 feet high, on the south side.

On the 7th of March a clear fluid was first found in a vessel attached below the quill (B), perhaps caused by rain which had fallen on the 6th, and had run down from the stem. On the 8th of March the water (exuded from the stem) trickled from B and C; D remained dry. The fluid gave neutral reaction with litmus paper. D did not become moist until the 11th, while B and C poured out abundance. The two last were closed and cemented with resin on the 12th; D was bored out 1 inch deep, and a new hole was made of the same depth,—

E, $2\frac{1}{2}$ feet from the ground, on the south side.

The sap flowed immediately from both; E delivered 70 drops in five minutes, D only 15. On the 13th new traces flowed from D; E gave 19 drops in five minutes. Both holes were stopped and two new ones bored,—

F, 6 feet high, north side.

G, 1 foot high, same side.

F gave only traces, while G gave 32 drops in five minutes. On the 14th F gave nothing, G 10 drops in five minutes. On the 15th F was dry; G gave 45 drops in five minutes. On the 14th a new hole was bored,—

I, 4 feet high, on the north side, which gave off no fluid on the 14th or 15th. All these experiments were made at noon. From the foregoing, the exudation and decurrence of the sap occurred observably earlier in the lower than in the upper part of the stem; it was caused by a warmer temperature.

All these fluids were tested for the ferrocyanide with sulphate or acetate of peroxide of iron, without results. It is evident that none of the holes entered the current of sap passing up from the root A (*vide infra*). On the 10th of March the ascending root A was cut off and examined. The section 5 inches above the point where it dipped in the fluid, reacted strongly with salt of iron and excess of hydrochloric acid, and the same occurred with the other parts; the ferrocyanide had even *descended* into the lateral branches of the root. The longitu-

dinal section showed that the liber had absorbed strongly; and light blue, not sharply defined streaks, corresponding to the course of the tracheæ, were seen in all parts of the wood; the thin pith remained unaffected. On the whole the reaction was weak, because the great mass of the fluid had already ascended into the higher parts of the plant.

2. A young sycamore stem (*Acer platanoides*), 3 inches in diameter, was watered with the ferrocyanide in the ground; but this could not be detected in a small quantity of fluid which exuded from boring. It appeared to have been wholly decomposed by the (ferruginous) soil, since this had acquired a blue colour.

3. The soil at the base of a young sycamore of $1\frac{1}{2}$ inch diameter was watered, on the 26th of February, with a weak solution of the ferrocyanide. On the 28th holes were bored into the stem, but the drops which exuded did not react with salt of iron; neither did the $\frac{1}{4}$ of a drachm of fluid that was found on the 1st of March. No more exuded after this. The soil around was coloured blue, and when the stem was cut off on the 10th, no ferrocyanide could be detected in it.

The small efflux of sap in these two young trees, 2 and 3, was remarkable.

4. The earth round the trunk of a sycamore, 4 inches in diameter and 35 feet high, was watered with solution of the ferrocyanide on the 2nd of March; a hole, A, was then bored in the stem 1 foot above the ground; the vessel attached to this was rapidly filled with fluid. Tolerable quantities of fluid flowed out, and in part down, continuously during the following days, but on the 7th of March no ferrocyanide could be discovered in it. On this day the soil round the tree was watered a second time with one ounce of a more concentrated solution; the orifice continued to pour out freely. On the 9th the soil was watered a third time, and a new hole was made (on the north side) at the same height as the old one (on the south side). On the 10th of March the fluid which had trickled from A gave a dark blue precipitate with sulphate of iron, which was not the case with B. On the 11th no reaction on either side. On the 12th no more had exuded; on the 14th therefore the tree was cut off at the base, and three pieces of it separated and examined, from the base, the middle, and the summit. The two lowest pieces

only gave a reaction, which was moreover very weak; the transverse section displayed a few light blue bleared spots in the wood; the liber and bark were unaffected. Longitudinal sections, on the contrary, displayed at particular spots, very sparingly, *sharply* defined blue points or even streaks (some of them in the direction of the medullary rays); microscopic examination showed that the few places in which some of the absorbed sap still remained, were *tracheæ* (spiroids) and the neighbouring prosenchyma of the wood. In the middle fragment, 10 feet above the ground, the cross section gave the same result as before; longitudinal sections led to none.

5. On a young sycamore, with a trunk $4\frac{1}{2}$ inches in diameter, a branch A, arising 7 feet above the ground on the north side, was bent down to a certain degree and fixed in this position, the outer part cut off, and the point of the portion remaining attached to the stem, dipped 4 inches deep into a cylindrical glass full of solution of the ferrocyanide. A hole B was bored, 1 inch deep, 1 foot above the ground on the south side of the trunk. This was done on the 2nd of March. On the 3rd the branch A had absorbed all the fluid, as far as it dipped in it; the glass attached under B was filled with watery fluid, which did not react with salt of iron. On the 5th the glass at A was refilled. On the 4th the vessel at B was only half-filled; on the 5th again quite filled; rain which fell on the 4th seemed to have increased the flow of the sap. By the 7th (warmer weather than the 6th) the glass A had been again emptied, and was filled anew. On the 9th again empty, but up to this day, when the efflux at B *ceased*, no ferrocyanide could ever be detected in the fluid poured out. On this day therefore a new hole C was bored at the same height as B, on the north side of the trunk, corresponding to the absorbing branch A; and in spite of B having stopped, fluid was poured out freely at C, which on the 10th reacted *deep blue* with the iron salt; the glass A was emptied down to a quarter of its contents (it held altogether about 1 cubic inch). On the 11th the freshly effused fluid exhibited a very strong reaction.

The here evidently strong *suction* of a *cut branch*, or of a cut root, as in Experiment 1, thus both in the *ascending and descending directions*, results from the pressure of the atmosphere.

The large surface of the tree with its hundreds of shoots causes an evaporation even before the buds swell; the vacuum resulting from this, causes any fluid which may be brought into free communication with the interior of the tree, at any spot, to be driven in by the *vis a tergo*. The power of suction thus produced increases in equal proportion as the surface of the shoots is increased by the presence of leaves, and the capacity of the air to retain moisture by the heat of summer, as Hales (Vegetable Statics) and, more recently, Dassen (Wiegmann's *Archiv*, xiii. 2. p. 311) have proved; under the most favourable circumstances it sustains a column of mercury 12 inches high. It will not be thought strange that the height of the column of mercury did not attain 18 inches, as has been observed in curved *glass* tubes under similar circumstances. The bark of the shoots of a tree does not form a solid envelope like the glass, for even with a smaller weight of the column of mercury, the air itself penetrates through the bark into the interior, and thus puts an end to all further ascent. Hence the loose-barked vine absorbs but weakly; the denser *Prunus domestica* raised a column to $\frac{1}{11}$th of a Flemish ell (6¾ inches); *Betula nana*, 0·240 (13½ inches) (Dassen). Hales observed the column rise to 4 inches in the vine, and 12 inches on an apple branch (equal to 13 feet 8 inches of water).

It is remarkable how accurately the fluids ascending or descending in this way are retained in that side of the stem which corresponds to the absorbing branch (or root); this is explicable by the straight, uninterrupted, little-branched course of the tracheæ; the anatomical examination of the preceding cases also proved this directly. The absorbing branch was cut off on the 11th of March and anatomized, with the following results. In a cross section 1 line above the lower end, which had been dipped in the fluid, *all* parts, bark, liber, wood and pith, reacted deep blue; but even at a distance of 2 lines the pith was found uncoloured! Four inches further up, that is, close above the upper boundary of that portion of the branch which had been immersed in the fluid, the heart-wood in the vicinity of the pith was also found uncoloured, as was the case everywhere above this. From this point the pitted and striped *trachea* of the softer external portion of the wood, with the *liber*, had taken on the conduction of

the fluid, and on reaction formed sharply defined dark blue lines, which could be easily traced even in the stem, both upwards and downwards, more than 1 foot from the absorbing branch. Microscopic investigation showed that the blue colour had only spread half or the whole width of a row of cells, around the tracheæ. A longitudinal section of the (upper) axil of the branch indicated the course of the tracheæ by curvilinearly arranged blue spots and streaks, and not by continuous blue lines. Consequently these tracheæ do not run so perfectly on one and the same plane here, that their entire course can be at once displayed by a single section. It is worth notice, that *only that side of the stem on which the branch was seated* was coloured blue, the opposite not at all.

That the *pith does not conduct*, is comprehensible, since the air it contains could not readily be displaced by water penetrating, and each of these cells containing air is a completely closed sac. But it is difficult to understand why the *medullary sheath* and the *heart-wood* do not conduct sap, since here communicating unrollable spiral and striped tracheæ are present in abundance. This non-conducting layer amounted, at the point of attachment of the branch, to a quarter of the woody layer (the entire diameter of the stem at this point amounted to 1¼ inch). It is certain that the air visibly contained in these tracheæ is no hindrance, for it is noue in those of the outer, younger wood. The elongated cells of the medullary sheath are far narrower and closer than the prosenchymatous cells of the wood; they are crowded with starch-granules, which are absent from the rest of the prosenchyma of the wood up to the medullary rays. Can it be some starchy or gummy mucilage which stops the progress of the fluid? I believe not; there is no dissolved starch present; iodine distinctly reveals the unaltered starch-granules. And as to gum, it is not evident how this could close up the tracheæ from the cells, since the microscope shows the former to be filled with air-bubbles.

6. *Repetition of the preceding experiment.*—On a sycamore trunk 3 inches in diameter, a branch A, at a height of 5 feet, was cut off, bent down, and fastened: the wound dipped in a glass of 1 cubic inch capacity, filled with concentrated solution of ferrocyanide of potassium. At the side (the south) of the

trunk a hole B was bored at 1 foot above the ground, and a glass attached to catch the exuding fluid. On the following day (March the 5th) the vessel at A was almost empty and was refilled. In the glass at B there was no fluid; but on March the 6th $\frac{1}{6}$th of a cubic inch, which *reacted deep blue* with sulphate of iron. On the 6th the glass A was only half empty, but was refilled. On March the 7th, at 2 o'clock P.M. (as usual), A was half empty; nothing had flowed from B, but the orifice reacted deep blue with salt of iron. A new hole C was bored $\frac{1}{3}$rd of a foot above the ground, on the east side, but no fluid exuded. On the 8th of March A was half empty; nothing had flowed from C. On March 9th A was quite empty; C had given off nothing.

The tree was cut down on the 9th of March in order to trace the course by which the fluid had descended from the absorbing branch to the orifice. The liber and albumen reacted blue, but not the bark, heart-wood or pith. In the albumen the colouring was streaky, and the microscope showed that it was in the tracheæ: these contained blue fluid with a few air-bubbles. The liber was not coloured nearly so far as the woody portion; at 3 feet down the stem from the absorbing branch (on the same side), the wood reacted very distinctly, but not the liber. From this it follows that *capacity of conducting* is much *inferior* in the *liber-layer*, to what it is in the tracheæ of the wood. Distinct reaction in blue streaks could also be observed in the trunk more than $2\frac{1}{2}$ feet above the branch, on the same side (but not on the other); here the liber was affected, although not so strongly. A transverse section showed that about $\frac{1}{3}$rd of the circumference of the trunk below the branch, $\frac{1}{4}$th above it, had taken part in the diffusion of the sap: the base of the branch occupied about $\frac{1}{3}$th of the circumference. Dissection of the point of insertion of the branch on the stem gave exactly the same results as in No. 5. Examination of the wood in the vicinity of the orifice, and 2 inches lower down by radial longitudinal sections, showed that the *tracheæ* had conveyed down the solution: the cellular tissue and medullary rays did not react.

It is evident, therefore, that both in normal absorption by uninjured roots, and in abnormal by wounds, the *conduction of the spring sap* occurs *chiefly through the tracheæ* and liber; a

result which stands in contradiction with the experiments already related on Monocotyledons and Acotyledons at the time of the full activity of the leaves (*vide infra*).

Comparison of the Experiments 5 and 6 with 4, shows how much more quickly the fluid runs through the tissues when it is placed in contact with *open wounds*, than when the absorption is allowed to take place in the normal way by the root. In 5 and 6 the ferrocyanide traversed some 8 feet, down from the cut branch to the orifice, in one day; in 4 it occupied seven days for the salt with which the soil (root) was watered to ascend to an orifice 1 foot above the ground. In the former there were open communicating tubes, in the latter closed membranes only permeable through endosmose.

7. In a young sycamore of about 3 inches diameter, a root on the west side, A, ½ an inch in diameter, was laid bare, cut through at the distance of a foot from the trunk, and the upper end placed in a cylindrical glass of 1 cubic inch capacity, containing solution of ferrocyanide. An orifice B was made at a height of 1 foot above the soil, on the south side of the trunk, and a glass vessel fixed under the quill introduced into it. On the following day (March 5th) the vessel at A was found empty, and was refilled; B was half full of fluid (½ a cubic inch). On March 6th, A, again empty, was again refilled; B contained ⅓rd of a cubic inch of fluid. On the 7th, A as the day before; nothing emitted from B. On the 9th, A empty. On the 10th, A was refilled; B contained fluid again (½ a cubic inch), evidently in consequence of warm weather the day before. None of the exuded fluid gave reaction with salt of iron. On the 11th, nothing emitted from B. A new hole C was bored on the west side, corresponding to the root A, 6 inches above the ground, but nothing flowed from it up to the 13th. Although, therefore, the fluid had been absorbed, it was impossible this time to draw it from the stem here by tapping; evidently because the orifice B, which alone emitted fluid, was not made on the corresponding side of the stem. The observations were made at 2 P.M. each day.

On the 13th of March the absorbing root was cut off and dissected. Reaction with sulphate of iron and hydrochloric acid showed that the exceedingly small pith had not conducted. At

a distance of about 10 inches from the immersed lower end (the root dipped in about 3 inches), the longitudinal section gave a blue reaction throughout the woody substance; the microscope showed liber, tracheæ and wood-cells stained; the tracheæ most strongly, both in the inner and outer parts of the wood. The solution had not only ascended, but also passed down as much as 2 inches in small lateral branches of this root. At these points the liber no longer took part in the conveyance of the fluid, while many (especially the central) tracheæ reacted deep blue.

It is worth notice that the (ferruginous) soil in the vicinity of the entire root acquired a blue colour from the 6th of March onward; perhaps by secretion through the peripherical parts of the root, perhaps through the injured points of the little radical fibres.

8. A sycamore trunk of $\frac{3}{4}$ of a foot diameter was bored with similar holes, 1 inch deep, in two places, and all the exuding fluid was caught.

A, orifice 1 foot from the ground, south side.

B, orifice 3 feet from the ground, south side, 1 inch further westward.

Experiment commenced at 3 o'clock on the 5th of March.

Five o'clock: A had emitted 1 Paris cubic inch of clear watery fluid; B $\frac{1}{2}$ a cubic inch.

March 6th, 8 A.M.: A and B had secreted nothing (cold night, below freezing point).

2 30 P.M.: A $9\frac{1}{4}$ cubic inches; B $12\frac{1}{2}$ cubic inches.

5 30 P.M.: A and B had each given off $\frac{1}{8}$th of a cubic inch.

March 7th, 8 A.M.: the flask at A and B empty.

2 P.M.: A $\frac{2}{3}$ths of a cubic inch; B $\frac{1}{3}$th of a cubic inch.

5 30 P.M.: the flasks at A and B empty.

March 8th, the same.

According to the foregoing, *night* limits the force of the current (by a lower temperature). When we reflect on the *unequal duration* of the bleeding in the trees 2—8, which all stood near together, it becomes a question what was the cause of this phænomenon?

The varying *thickness of the trunk* does not seem to explain the matter. No. 4 was 4 inches in diameter and bled ten days; No. 2 was 3 inches in diameter and bled five days; No. 8 was

9 inches in diameter and bled only three days. Neither does the *height of the orifice* above the soil explain the phænomenon, for the period of bleeding differed much at equal heights, as No. 8 and No. 4 show. Just as little influence is exerted by the aspect of exposure.

On the other hand, the higher or lower *position* of the trees appeared to have an essential influence hydrostatically. They all stood on the southern slope of a hill 30 feet high, in the Botanic Garden at Giessen, in the following order, from above downwards:—

a,	No. 8,	which bled 3 days.	
b,	— 2,	....	5 ..
c,	— 5,	....	5+3 days.
	6,	....	4 ..
d,	— 3,	....	2 ..
	— 7,	....	7 ..
e,	— 4,	....	10 ..

No. 4 stood 5 feet above the bottom of the hill, and was 35 feet high; the rest were only about 27 feet, in spite of their unequal diameter. This difference of *height* also appeared to have some influence.

The epochs of tapping the different trunks were not far enough apart for me to ascribe any considerable importance to that point.

9. A trunk of *Acer campestre*, 1½ foot in diameter (at the bottom), was tapped at equal depths of 1 inch, in two places, at 3 o'clock on the 5th of March, and the exuding fluid all collected (as in all cases, with care that no rain-water should penetrate):—

A, orifice 1 foot from the ground, south side.

B, the same, north side.

By about 5 o'clock A had delivered 1⅗ths of a cubic inch, B also 1⅗ths.

From that time till 8 A.M. on the 6th of March not a drop flowed out. About 2 o'clock there were 13⅘ths cubic inches in A, and 19¼ cubic inches in B. At $5^h\ 30^m$ there was ½ a cubic inch from each. On the 7th at 8 o'clock there was no fluid. At 2 o'clock there was ⅕th of a cubic inch at A, ½ a cubic inch at B. At 4 o'clock no more had flowed out; neither was there any at 2 o'clock on the 8th. From the little that the short duration of the bleeding allowed to be observed here, the north side would

appear to pour out more sap than the south. The checking influence of nocturnal cold was again distinctly visible here.

10. On the 10th of March a young sycamore stem (*Acer platanoides*), 3 feet high and ½ an inch in diameter, was plentifully watered with solution of ferrocyanide of potassium. On the 15th it was taken up, root and all. When dissected, the reagents showed that absorption had not commenced in the stem. At the base alone, weak, bleared blue spots were produced on a cross section. In one place the colour was deep and sharply-defined enough to admit of microscopic examination: this proved that the walls of a few streaked and spotted tracheæ were coloured blue.

11. A white birch, with a trunk 1 foot in diameter, was tapped 1 foot above the ground, on the west side, on the 4th of March; up to the 11th nothing flowed out. On this day a new orifice was made in the west side of the stem, at a height of 7 feet. Up to the 14th neither gave off any liquid. Only a few sucking flies appeared to indicate that the sap was beginning to rise.

It is worthy of notice, how much later the bleeding occurs in the birch than in the sycamore.

12. On the 7th of March, at three o'clock, a sugar maple (*Acer saccharinum*), with a trunk 1½ foot in diameter, was tapped:—

A, orifice 1 foot from the ground, south side.

B, orifice 5 feet from the ground, south side, but 1 inch further to the east.

About eight days previously several small branches had been cut off further up the stem; some sap ran down from the wounds. The fluid exuding from the borings was collected, and gave the following results:—

March	7.	3½	o'clock, at A,	3	cub. in.;	at B,	1½	cub. in.
—	..	5½	....	3½	....	....	7½	....
—	8.	8	....	16½	....	....	a few drops.	
—	.	2	....	8¾	....	....	4	cub. in.
—	..	5½	....	11	....	....	4	....
—	9.	7½	....	6½	....	....	none.	
—	.	2½	....	17	....	....	7¾	cub. in.
—	.	5½	....	7½	....	....	2½	....

March	10.	$7\frac{1}{2}$	o'clock,	at A,	3	cub. in. ;	at B,	$1\frac{1}{2}$	cub. in.
—	..	$1\frac{1}{2}$	....		38(!)	....	....	11	....
—	..	5	....		9	....	....	4	....
—	11.	7	....		$13\frac{1}{6}$	....	....	$\frac{1}{4}$	....
—	..	2	....		9	....	....	$1\frac{1}{2}$	....
—	..	$5\frac{1}{2}$	....		$5\frac{1}{4}$	....	....	$\frac{3}{4}$	....
—	12.	7	....		4	....	....	$\frac{1}{2}$	....
—	..	2	....		17	....	....	$3\frac{1}{8}$	....
—	..	5	....		$4\frac{1}{2}$	....	....	$\frac{1}{2}$	....
—	13.	$7\frac{1}{2}$	....		$6\frac{1}{2}$	....	....	a few drops.	
—	..	2	....		$15\frac{1}{2}$	....	....	1 cub. in.	
—	..	$5\frac{1}{2}$	....		$4\frac{1}{2}$	....	....	a few drops.	
—	14.	$7\frac{1}{2}$	....		$13\frac{1}{2}$	....	....	ditto.	
—	..	2	....		23	....	....	$2\frac{1}{2}$	cub. in.
—	..	$5\frac{1}{2}$	....		1	....	....	none.	
—	15.	$7\frac{1}{2}$	....		none.	....	....	none.	
—	..	11	....		5	....	....	$\frac{1}{5}$	cub. in.

From this it follows that the efflux, or fulness of sap, is greater in the lower part of the stem than further upwards. This phænomenon is not hydrostatical (as a barrel emits a more powerful stream from a hole nearer the bottom, than from one at the top, on account of the higher pressure of water), but depends on the force of the water making its way *upwards*, as is seen by a comparison with Experiment No. 1. It is also again seen what an obstacle the nightly cold is. Lastly, a comparison of the temperatures of the air in the sun, which I observed, shows how much the ascent of the sap is *favoured by the heat of the air*.

From the following table, especially from the two last columns, it is seen that on the whole the outflow runs parallel with the temperature. The 10th of March alone forms an exception, evidently on account of the unusually favourable weather on the 9th, the after-influence of which is seen here.

SUMMARY.

	Sum of the Temperature of the Air in the Sun.		Amount of Heat per hour.	Efflux of Sap per hour.
	At the Hours	Degrees of Fahrenheit.		
Mar. 7. from $3\frac{1}{2}$ to $5\frac{1}{2}$ A gave $5\frac{1}{2}$ cub. in.	4 and 5.....	63·5 and 54·5 ..... = 54°	27°	$1\frac{3}{4}$ cub. in.
— 8. ... 8 ... 2 ... $8\frac{3}{4}$ ...	9, 10, 11, 12, 1, 2...	45·5—47·75—47·75—52·25—72·5—81·5 ..... = 155·25	25·825	$1\frac{1}{2}$ ...
— ... ... 2 ... $5\frac{1}{2}$ ... 11 ...	3, 4, 5	83·75—72·5—63·5 ..... = 123·75	41·25	4 ...
— 9. ... $7\frac{1}{2}$ ... $2\frac{1}{2}$ ... 17 ...	8, 9, 10, 11, 12, 1, 2	45·5—47·75—52·25—77—86—88·25—88·25 ..... = 261	37·25	$2\frac{3}{7}$ ...
— 10. ... $7\frac{1}{2}$ ... $1\frac{1}{2}$ ... 38 ...	8, 9, 10, 11, 12, 1	41—43·25—45·5—47·75—50—56·75 ... = 282·25	15·375	$6\frac{1}{3}$ ...
— 11. ... 7 ... 2 ... 9 ...	8, 9, 10, 11, 12, 1, 2	41—41—43·25—43·25—43·25—43·25—61·25 ..... = 92·25	13·176	$1\frac{2}{7}$ ...
— ... ... 2 ... $5\frac{1}{2}$ ... $5\frac{1}{2}$ ...	3, 4, 5	70·25—61·25—43·25 ..... = 78·75	26·25	$1\frac{3}{4}$ ...
— 12. ... 7 ... 2 ... 17 ...	8, 9, 10, 11, 12, 1, 2	38·75—38·75—42·125—43·25—47·75—53·375—68 ..... = 108	15·428	$2\frac{3}{7}$ ...
— 13. ... $7\frac{1}{2}$ ... 2 ... $15\frac{1}{2}$ ...	8, 9, 10, 11, 12, 1, 2	43·25—44·375—46·625—46·625—52·25—50 ..... = 104·625	14·946	$2\frac{3}{14}$ ...
— ... ... 2 ... $5\frac{1}{2}$ ... $4\frac{1}{2}$ ...	3, 4, 5	47·75—47·75—45·5 ..... = 45	15	$1\frac{1}{2}$ ...
— 14. ... $7\frac{1}{2}$ ... 2 ... 23 ...	8, 9, 10, 11, 12, 1, 2	45·5—50—63·5—79·25—77—74·75—74·75 ..... = 240·75	34·391	$3\frac{2}{7}$ ...
— ... ... 2 ... $5\frac{1}{2}$ ... 1 ...	3, 4, 5	65·75—46·625—43·25 ..... = 59·625	19·875	$\frac{1}{3}$ ...
— 15. ... $7\frac{1}{2}$ ... 11 ... 5 ...	8, 9, 10, 11	36·5—41—62·375—55·625 ..... = 67·5	16·875	$1\frac{1}{2}$ ...

The specific gravities of the effused fluid exhibited the following scale. They were determined in a narrow-neck globular bottle, of about 1 oz. capacity.

Rain water, 1st filling . . . 25·660 grammes.
... ... 2nd ... . . . 25·661 ...
... ... 3rd ... . . . 25·665 ...

Sap of the Sugar Maple.

	Orifice A.	Orifice B.
March 7. 3½ o'clock	25·877 gramm.	
— 8. 4	25·875	25·918 gramm.
— 9. 2½	25·871	
— 10. 2	25·861	
— 11. 2	25·889	
— 12. 2	25·883	25·918
— 13. 2 ...	25·890	
— 14. 2	25·896	

According to this, the specific gravity increases pretty rapidly, and the sweetness of the sap also is readily detected by the tongue. The *upper* part of the stem contains a *less aqueous* sap than that near the soil.

The *reaction* of the exuded fluid was neutral to blue litmus and to turmeric paper in a fresh condition on the 8th of March; on the 9th slightly acid, as also on the 15th.

The *amount of sugar contained* was tested by adding solution of potash, a few drops of solution of sulphate of copper, and boiling; after a long-continued boiling only was a very small quantity of copper reduced. Some ammonia was set free in this operation. When the mixture was merely allowed to stand at ordinary temperatures, not the least copper was reduced in two hours. It was therefore cane-sugar.

13. A birch (*Betula pubescens,* Ehrh.) was tapped in two places at half-past two o'clock on the 8th of March. The base of the trunk was 1½ foot in diameter.

A, orifice 1 foot from the ground.
B, ... 7 feet ... .

Both orifices 1 inch deep. Quills were cemented in and the effused fluids caught. On the upper part of this birch a few small branches had been cut off, from which some sap exuded, which, however, did not run down to the bottom. The following quantities flowed out:—

March	8.	Up to	4	o'clock at A,	$9\frac{1}{2}$	cub. in.; at B,	7	cub. in.
—	..	..	$5\frac{1}{3}$	....	7	.. ....	4	..
—	9.	..	$7\frac{1}{2}$	....	$39\frac{1}{2}$	.. ....	$8\frac{1}{4}$	..
—	..	..	$2\frac{1}{2}$	....	$23\frac{3}{4}$	.. ....	?	..
—	..	..	$5\frac{1}{7}$	....	9	.. ....	6	..
—	10.	..	$7\frac{1}{2}$	....	$5\frac{3}{4}$	.. ....	$1\frac{1}{7}$	..
—	..	..	2	....	$18\frac{1}{6}$	.. ....	$15\frac{1}{3}$	..
—	..	..	5	....	7	.. ....	$12\frac{1}{2}$	..
—	11.	..	7	....	$13\frac{1}{2}$	.. ....	$4\frac{1}{2}$	..
—	..	..	$2\frac{1}{2}$	....	$9\frac{1}{3}$	.. ....	$\frac{1}{3}$?	..
—	..	..	$5\frac{1}{2}$	....	$3\frac{1}{2}$	.. ....	$6\frac{1}{5}$	..
—	12.	..	$7\frac{1}{2}$	....	$5\frac{3}{4}$	.. ....	$7\frac{1}{2}$	..
—	..	..	2	....	$19\frac{2}{3}$	.. ....	38	..

As there was no fixed result here, the holes A and B were bored out again to remove any accidental obstruction.

March	12.	Up to	5	o'clock at A,	5	cub. in.; at B,	9	cub. in.
—	13.	..	$7\frac{1}{2}$	....	$9\frac{3}{4}$	.. ....	$31\frac{1}{2}$	..
—	..	..	2	....	$4\frac{3}{4}$	.. ....	33	..
—	..	..	$5\frac{1}{2}$	....	2	.. ....	12	..
—	14.	..	$7\frac{1}{2}$	....	$6\frac{1}{3}$	.. ....	$39\frac{1}{2}$	..
—	..	..	2	....	$3\frac{1}{3}$	.. ....	$39\frac{1}{2}$	..

A was closed up, and a new hole C bored near it.

March	14.	Up to	$5\frac{1}{2}$	o'clock, from C,	5	cub. in.; from B,	$1\frac{1}{4}$	cub. in.
—	15.	..	$7\frac{1}{2}$	....	$\frac{8}{9}$	.. ..	none.	
—	..	..	11	....	3	.. .	4 drops.	

Thus, from the 8th to the 11th of March more flowed from below; from that time the proportion was reversed, perhaps in consequence of the more powerful *swelling* of the lower (*wetter*) *wood* at A, and a contraction of the orifice resulting from this. After a new hole was bored, the proportion was as in ordinary cases (compare Experiments 20 and 21).

The specific gravities of the fluids from A, B, and C, exhibited the following scale:—

March	8.	Spec. grav. of A,	25·705	gramm.; of B,	25·715
—	9.	....	25·690	...	
—	10.	.. ..	25·712	..	
—	11.	.	25·728	.	
—	12.	.	25·722		
—	13.	.. .	25·718	. ..	25·717
—	14.	...	25·714	.. .	25·719
—	15.	Spec. grav. of C,	25·732	....	

According to this, there was increase at A from the 9th to the 11th, then from the 12th (through a fall of snow on the 11th) decrease; on the 15th increase (through the preceding warmth, and resulting evaporation of moisture from the earth?); at B increase. The sap from the lower orifice was not so dense as that from the upper.

The *reaction* of the fresh sap was neutral to blue litmus and turmeric papers on the 8th and 9th of March; on the 15th slightly acid.

On the 8th and on the 15th the taste was indistinctly sweetish and earthy; but chemical testing demonstrated the presence of *grape*-sugar, when the fluid was warmed with solution of pot-ash and sulphate of copper, since a red powder was rapidly thrown down.

14. A birch (*Betula pubescens*, Ehrh.) $1\frac{1}{2}$ foot in diameter was tapped in various places, in order to discover whether more fluid was effused from the upper or lower part of the stem. This took place on the 14th of March, at three o'clock.

A, East side, $1\frac{1}{2}$ foot high, gave in 5 minutes 335 drops.
B, .. 8 feet .... 120 ..

A and B were then closed.

C, North side, 2 feet high, gave in 5 minutes 118 drops.
D, .. 8 .. .... 80 ..

The lower orifice therefore gave more than the upper.

The fluids of A and B were neutral with test-papers.

15. Repetition of the preceding experiment in another birch of the same species and of the same size. Experiment made after three o'clock on the 14th of March.

A, N.E. side, 1 foot from the ground, gave in 5 minutes 93 drops.
B, .. 9 feet .... 103 ..

A and B were closed, and two new holes bored.

C, North side, 1 foot from the ground, gave in 5 minutes 63 drops.
D, . 9 feet .... 51 ..

Here also the lower orifice usually emitted more than the upper. The striking and frequent anomalies which appeared here, as in Experiment 13, will appear abundantly explicable when we reflect what an important influence a very small difference in the condition of the orifices (in regard to depth, diameter, quan-

tity of fragments of wood remaining in, &c.) and the unequal expansion of the wood must have; a difficulty which I could not master. Here, therefore, useful results could only be obtained by a number of observations.

II. The Summer Sap.

The circulation of the sap during the summer, at the period of the greatest activity of the leaves, displays at once much agreement with and many striking differences from that of the early spring, among the latter of which stands above all the circumstance that the trees hitherto mentioned no longer bleed from wounds inflicted on them, although, as a little reflection must reveal, the quantity of fluid actually passing in the stem is far greater; a fact also demonstrated by direct observation.

In summer, as in spring, there exists a rapid ascent of the crude sap; in addition to this, a descent of unelaborated fluids after every shower of rain; and, lastly, a descent of the elaborated fluids from the leaves into all parts of the plant.

Since there apparently exists no means of tracing accurately the mode and course of the last phænomenon directly, I have restricted myself to the first, namely to the roads which the unelaborated fluids traverse in their ascent and descent in plants; but the results obtained could not but give ground for the deduction of many conclusions as to the behaviour of the elaborated saps. The following pages therefore will be devoted to the investigation of the paths by which the crude summer sap ascends or runs down under conditions as natural as possible, and afterwards also under various abnormally arranged conditions, especially when wounds have been made in the plant.

A. The Ascending Sap.

1. *With* normal *absorption of the Sap by the Root.*

For the purpose of tracing the course of the sap, the earth round the plants to be experimented on was watered with dilute solution of ferrocyanide of potassium; after which cross slices of the plant were tested for that solution with a mixture of acetate of iron and hydrochloric acid. It is not advisable to make these experiments on plants standing in the open ground, since the

fluid is here spread about too much and too unequally; hence the absorption becomes very uncertain, or even fails to take place at all, as I have experienced several times to my discomfort in vines, plums, and sycamore trees. I therefore preferred such plants as had been kept a longish time in pots, taking only such as exhibited a full activity of vegetation.

Euphorbia terracina, L.—Watered on the 5th of June; taken up by the root on the 8th. The saline solution was detected in the inner layer of the bark (the liber), and in a few tracheæ or spiroids of the outer layer of wood. Watered on the 15th; withering on the 24th; taken up on the 25th; the saline solution could be detected last, as far as $2\frac{1}{2}$ inches above the collar of the root, in the striped spiroids of the outer layer of wood and in the liber, in which it ascended farthest. These vessels were only partially filled with the saline solution; the majority still contained air and did not react.

Since in these and several similar cases, not only the cellular tissue, but also—in direct opposition to the preceding observations on the Monocotyledons—the air-vessels took part more or less in the conduction of the sap, the first object was to clear up the contradiction.

The Monocotyledons used in my investigations, whatever their other differences, were almost without exception furnished with tuberous or bulbous rhizomes. The conjecture was not far-fetched, that the predominant subterraneous stem-structure, the whole character of which is, moreover, accumulative and retentive, retarded the conveyance of the fluid into the upper portions of the stem, and thereby exerted essential influence over it. Hence arose the question, whether, in the Dicotyledons also, varied conditions in the conduction of the sap would occur according to the rapidity of the absorption, according to superabundant or scanty watering, &c.

a. *Accelerated absorption of the Fluid.*

Balsamina hortensis.—The root was carefully freed from earth and immersed in a large vessel full of solution of the ferrocyanide; then the stem was cut across obliquely at a height of 8 inches, and sucked with the mouth. After the sucking had been continued for half an hour, reaction occurred at this point;

the solution had penetrated into several of the large and small spiral vessels of the stem, and still more had ascended in the delicate parenchymatous tissue surrounding the vascular bundles; the pith and remaining portions of the cellular tissue had taken no part. When the lower end of a fragment of a balsam stem 3 inches long was dipped in ink and the upper end sucked, the ink rose *instantaneously*. From this is evident how considerable an obstacle the uninjured epithelium of the root opposed to the forced penetration of the fluid in the preceding case.

Balsamina hortensis.—The plant was allowed to stand dry from the 14th to the 19th of June, until the withering stem had collapsed considerably. The soil was then well watered with 14 cubic inches of dilute solution of the ferrocyanide, which was wholly retained by the mould, as in a sponge (the plant stood in a pot 5 inches high and 4 inches in diameter). On the 21st it began to wither, the leaves exhibited spots and died, while the stem was still partly elastic. On the 23rd the plant was analysed. All parts had absorbed. In the cellular tissue of the pith and rind, the *intercellular spaces* or passages, especially, were found deep blue, so that the rind-cells which contained a red sap, presented red spots enclosed in blue frames; in the pith the whole of the *cell-contents* were coloured blue in many places. The *vessels*, striped as well as unrollable spirals, together with the immediately adjacent prosenchyma, were almost without exception dyed deep blue; air-bubbles were met with in very few, but sometimes even in those vessels which contained blue fluid.

b. *Retarded absorption of the Fluid.*

Oxalis tetraphylla.—Watered very slightly with the saline solution from June 25th to July 27th; the plant was exposed to the atmospheric moisture in the open air. About this time the leaves began to lose their colour and wither.—Analysis. The bulb is composed of two distinctly separated circles of scales, from the interior of which springs the leaf-stalk. The solution was principally met with in the periphery of the inner portion of the bulb; and the elongated *cells* at the surface of the separate fleshy scales, but not the spiroids, had also absorbed it in very small quantity.—Leaf-stalk. This contained a loose circle of

five vascular bundles; the salt had ascended in the prosenchymatous cellular tissue surrounding these, but not in the tracheæ themselves; the latter were filled with air. The cortical layer had also conducted, and indeed in the intercellular passages.

Euphorbia terracina, L.—Treatment as in the preceding case; taken up at the end of four weeks. The solution had ascended in small quantity, especially in the inner cortical layer, the liber. No saline solution in the vessels of the wood.

Hibiscus Trionum.—Watered with 1 cubic inch of the saline solution during heavy rain; taken up after three days. Only the root had absorbed up to this time, and chiefly in the central layer of wood, where the prosenchymatous cells in the vicinity of the vessels were coloured blue in spots: the tracheæ took no part.

These experiments showed that when small quantities of liquid are absorbed by the root, the sap of herbaceous Dicotyledons ascends, just as in the Monocotyledons above described, in the *cellular tissue*, and with especial ease in the delicate prosenchyma surrounding the vessels; while when the absorption is hastened and superabundance of fluid present, the *vessels* also take part in the conduction of the sap, at the same time proportionately parting with the air they contain.

2. *Behaviour of the Ascending Sap in* ABNORMAL *absorption.*

Salix alba.—Absorption through the exposed *wood*.—A young leafy shoot 10 inches long was stripped of its bark for 2 inches at the bottom, and dipped 1 inch in the solution; 2 inches of bark were also removed at the upper end, and this part rolled up in blotting paper. Then, to prevent drying, a glass tube closed at the upper end was passed over the upper half of the shoot. After one day the paper was already moist and reacted strongly blue; after six days the shoot was analysed; it was filled in all parts with the saline solution, especially, however, in the wood-vessels which were gorged with sap up to the very top; much salt had crystallized out on both surfaces of the leaves, especially at the bases. Here, with the mouths of the vessels of the wood standing open, a rapid ascent was observed not only in the longitudinal direction, but also *horizontally*, into the blotting paper in contact only with the alburnum.

Salix alba.—A young leafy shoot 12 inches long was stripped of its bark for 2 inches at the bottom, and dipped 1 inch in the fluid; 1 inch below the top (the upper oblique cross section of the shoot) an annular piece of bark 3 lines wide was removed. Protected from drying as before. After six days the salt was found to have ascended into the very apex, and indeed into *all* parts, but most strongly in the medullary sheath. This contained dark blue dotted vessels and unrollable spirals. Only the epidermis of the upper piece of bark gave no reaction.

S. alba.—A piece 12 inches long was cut out of a young leafy shoot, 2 inches of bark removed at the bottom, and dipped 1 inch into the solution. In the upper part a little ring of bark was cut out, and the whole allowed to stand *without* protection from evaporation. After six days, all parts, up to the top of the shoot, even the externally dry, exposed part of the wood which had been laid bare, gave a reaction. At the extreme point the vessels of the medullary sheath no longer took part, but the inner prosenchymatous cells of the wood reacted deep blue.

From these experiments it is seen how little share the bark takes in the conduction of the sap, and how readily a horizontal movement of the sap takes place from the gorged young wood into the bark.

S. alba.—Absorption through the *bark.*—A piece 12 inches long, of a young leafy shoot, was taken and the bark slit up 2 inches from the bottom drawn back, and the exposed cylinder of wood, 2 inches long, removed; then the lower end (merely bark) was dipped 1 inch into the solution. After six days the shoot was found remarkably dry, from insufficient supply of fluid.—Analysis. The whole of the stripped piece of bark, even the epidermis, reacted strongly. The wood had likewise absorbed fluid from the bark into *all* parts at the lower end, but not uniformly; particular vessels and cells did not react at all. —Cross section 2 inches higher up. The bark and medullary sheath had absorbed most, the pith least. At 3 inches distance from the lower end of the wood, the salt was found only in liber and wood; the epidermis and pith no longer reacted.

Consequently, under favourable circumstances, a movement of the fluids in the bark, and *horizontally from the bark* into the wood, undoubtedly occurs, although to a very slight extent

The isolating power of the epidermis against moisture is worthy of notice.

B. The Descending Sap.

It seemed advisable in this case also to examine the different conditions separately, since it must be influential whether the fluids ascend from the uninjured roots before descending from the peripherical parts of the stem, or make their way down directly from the leaves, or from the points of cut shoots, &c.

1. *The Descending Sap when absorbed through the* LEAVES.

To warrant this experiment on physiological grounds, it suffices to refer to the fact of such a condition occurring in nature in every fall of dew or rain, wherein it in fact constitutes a condition essential to the well-being of plants.

Salix fragilis, L.—On June 7th a large uninjured leaf was immersed in the solution, and on the 10th the shoot which bore it was cut off.—Analysis. In the outer part of the shoot *all* the systems reacted; nearer the base at length only *isolated tracheæ* of the wood, and to the greatest distance on the *side of the twig on which the leaf arose.*

S. fragilis, L.—Experiment as before, with the modification that the larger shoot which bore the absorbing twig was notched deeply on the corresponding side. In three days the solution could be traced in the absorbing twig, farthest in the dotted vessels of the woody layer, and above all in the unrollable spirals of the *medullary sheath.* In the main shoot the fluid had descended over the boundary between the inner and outer layers of wood, *but not beyond the notch.*

S. fragilis, L.—Fresh leaves of a young twig were immersed one after another for several days in the solution, until a large quantity of it had been absorbed. The main shoot which bore the absorbing twig was ringed 3 lines broad down to the wood, and the ring of bark removed.—Analysis after twelve days. In the peripherical part of the absorbing twig all systems had again absorbed, but only the medullary sheath conducted far down; from this the fluid had passed out to the cicatrices of the partly fallen leaves, while the buds in the axils of these, at that time without any vascular connexion with the medullary sheath, were wholly passed over. It had descended a good way in the

interior of the wood of the *main shoot*, and here again at the *boundary between the outer and inner layers of wood* (but especially in the *latter*), while in the bark and liber it had *not reached* the ringed portion, much less passed beyond it. The fluid had, moreover, not merely descended, but also *ascended*, in the main shoot, and in the *same region* of the woody system. In the absorbing twig itself it likewise passed into the leaves situated below the absorbing leaves, and could readily be detected in the unrollable spiral vessels of their petioles. It must be observed that the two layers of the wood differed very much in their whole character; the outer was gorged with sap and evidently still in active process of development (June 27th), while the inner was white and dry, and therefore much better fitted to convey the crude juices. It therefore only remains remarkable, that the fluid which penetrated most easily in the *medullary sheath* of the twig, *left the neighbourhood of the pith in the main* (older) *shoot*, and passed to vessels situated further out. I observed the same in *Salix acuminata*, Smith, in which the solution was traced through three communicating generations or systems of branches. The still green absorbing twig behaved as above; the shoot from which this arose possessed three layers of wood; in this also the fluid had descended chiefly near the pith. The second shoot passed into (or arose from) a third thicker branch in the wood, in which four layers could be distinguished, and here the fluid had passed down at the boundary between the inmost and the next succeeding layer of wood, and not next the pith. It perhaps would not be erroneous to attribute this circumstance to the difference of the annual course of growth, assuming that the fluid always kept to one and the same tract, to vessels of the same age, in passing from the youngest shoot into the older. At all events this is not contradicted by the observed occurrence of *several* layers of wood, for I have seen distinctly (in *Salix alba*) that at least three succeeding systems (or generations) of shoots may be developed in one and the same year, the lowest and thickest containing two clearly distinguishable layers of wood, which however were indicated even in the last and thinnest (in the beginning of July). In order therefore to obtain a surer basis for the decision of the differences of age in the young systems of branches, I examined the condition of that small

vascular bundle which diverges at certain points from the medullary sheath, and runs into the petiole of the leaf which subtends the bud. Subsequently (in the succeeding year), these vessels, which are torn off externally at the fall of the leaf, are covered up and buried by degrees by the new wood formed in the young shoot (produced by that axillary bud); but they may still be discovered, even in old branches, if carefully sought. In the above case, in *Salix acuminata*, it was found that the saline solution had descended in the old main shoot, as mentioned, between the innermost and next succeeding layer of the wood, and thus *externally* over that little vascular bundle (originally going to a leaf) belonging to the inmost layer of wood.

Balsamina hortensis.—The solution absorbed by the leaves could in three days be traced upwards in all parts and farthest, and downwards in the vessels and the (wood) prosenchyma accompanying them; the *latter*, however, had conducted very much more fluid, since in cross sections the colourless large vessels were ordinarily perceived surrounded by a delicate ring of very small blue cellular points. In another case also, when the plant had absorbed very little of the solution, it was observed that this had descended principally in the internal cortical layer, and in the prosenchymatous cells in the vicinity of the vessels, not however in the latter themselves.

While, therefore, the tracheæ conducted most readily in woody plants, in the succulent balsam the neighbouring prosenchymatous cells were decidedly overcharged. Perhaps the cause lay in the prosenchymatous cells of the woody plants being in many cases filled with air (which is not the case in the balsam), whereby, of course, the passage of the solution from cell to cell through the, moreover dry, membranes might be rendered more difficult.

Lactuca sativa.—The solution absorbed by the leaf during eleven days was contained in especial abundance in the spiral vessels and their surrounding prosenchyma, on the corresponding side; on the other side of the stem, however, only in the prosenchyma surrounding the vessels, and in the lower parts of the stem the same. Here, moreover, the rind and the pith also had conducted, the pith principally in the cells at the boundary of the medullary cavity.

Euphorbia terracina, L.—After four days' absorption through

a leaf, the solution was traced in the entire stem, chiefly in the wood cells and isolated tracheæ (unrollable spirals and dotted vessels), which latter also contained a few *air-bubbles at the same time.*

Tropæolum majus.—After five days' absorption the solution was found inside the intercellular passages of the rind and pith, still more in the prosenchyma of the wood, and most of all in some trachcæ.

Cucumis Melo.—After one day's absorption all the intercellular passages, for several inches upwards and downwards in the stem, were found filled with the saline solution, while the fluid cell-contents themselves did not react; particular portions of the (wood-) prosenchyma, and above all some of the large tracheæ, had also absorbed.

The size of the vessels here permitted a decision, for this and all other cases, of the question whether the blue reaction so often observed in the interior of the exposed tracheæ might not result from the process of preparation, in short from the cutting of the sections, since the knife might indeed readily spread reacting fluids from the neighbouring prosenchymatous cells into the open mouths of the vessels. If such were the case, if therefore the reaction in the interior of the vessels were exclusively caused by an unavoidable smearing at the time of the analysis, the blue vascular points arising from the reaction would not, at all events, always occupy the same place in a succession of transverse slices from a stem where the course of the vessels was exceeding straight. *But this actually took place*, and it follows beyond doubt that the tracheæ can in some cases take up and carry forward fluids.

Vitis vinifera.—Here again it was found that the fluid proceeded both downwards and *upwards* from the absorbing leaf into the shoot bearing it, and in both cases in the same situation, namely, chiefly in the medullary sheath and in the portions of cellular tissue enveloping the liber-bundles on the inner side; apparently somewhat more had descended externally, and somewhat more ascended internally.

Cucurbita Pepo.—This time a *tendril*, instead of a leaf, was immersed in the solution, but it absorbed very little, probably in consequence of continued wet weather. Analysis showed

that the fluid had ascended in the prosenchyma accompanying the vessels, but not in these themselves.

From these and similar experiments it follows that in the absorption of fluids through the leaves, they are conveyed most readily by the tracheæ or the prosenchyma closely surrounding these; in plants gorged with sap more readily in the latter, and the reverse in dry woody plants. But even in the most succulent vegetables, only a somewhat longer continuance of the introduction of the fluid, or a greater quantity of it, is requisite to cause it to pass very readily into the air-tubes, and at length into all parts. It would therefore be erroneous to assume that any particular anatomical system is exclusively charged with the conveyance of unelaborated fluids in the ascending or descending direction. It was above all seen, that the tracheæ do usually convey air in summer, but very readily become temporarily more or less, or even wholly filled with fluids which displace the air. In fact, chemical reasons led me to consider the existence of the gas in the spiral vessels and spiroids as nothing more than a result of the absorption of crude fluids from the soil, which, ascending in the higher and warmer layers of the plant, at once give off almost unaltered the gases dissolved in them, these being diffused through those communicating passages, and so gradually evaporated outwards and upwards, without doing any mischief. In this point of view the vessels would be regarded as 'tubes of safety.'

It merits some attention, that, as the last experiments prove, no parts take so little share in the conduction of the solution downward as the layers of the bark. I therefore took occasion to investigate the capability of the bark to convey fluids by a direct experiment. This was done by removing every other passage but the bark from the descending fluid.

Salix vitellina.—On the 19th of June a fresh pendent twig 1½ line in diameter, had the bark slit up for the length of 1 inch at the side, 5 inches from the end; the bark was turned back and the wood within completely removed for a length of 2 lines; then the bark was returned into its place, rolled up in a living leaf to prevent drying, and the shoot strengthened by a splint. Lastly, a leaf situated below the excised wood was immersed in the solution. After twenty-four hours the fluid had advanced

very little in the pith, but elsewhere in all parts (bark and liber included) as far as the cross-section of the wood, but not beyond this even in the bark. The result was similar after absorption for four days. Even after seven days' absorption, the solution had not made its way over the bridge of bark; indeed this did not itself react, although it was in part perfectly fresh and living. In this case, moreover, the whole of the lower outer part of the twig was densely filled with the saline solution; even the badly conducting pith of the lower portion of wood reacted distinctly; the medullary sheath and the peripherical portion of the wood reacted most strongly, especially on that side of the wood corresponding to the absorbing leaf. From this it is evident that a far stronger penetration of the fluids than that which occurred here, is requisite to overcome the *resistance* which liber and bark oppose to the descending sap (see Sect. 4 below).

This observation rendered it necessary to apply the saline solution immediately to those parts to which the business of conveying the sap down is most frequently attributed, in order to bring the question nearer to a decision.

2. *The Descending Sap with direct absorption by the* CAMBIUM *layer.*

Salix acuminata, Sm.—In a branch 1½ inch thick, the bark was slit up, separated to a certain extent, and a piece of filtering paper, many folds thick, soaked in the solution, inserted under it, the wound being then loosely bandaged. After one day (June 15) it was found that the salt had *neither ascended nor descended beyond* the exposed portion of the wood; it had only penetrated extremely superficially even in the liber which lay directly upon the paper, and not at all into the rest of the bark or the wood.

Salix arbuscula, Whlbg.—Bark slit up for 2 inches; branch 1½ inch thick: otherwise as above. After four days, only those parts directly in contact with the paper reacted; the salt had not passed beyond in any direction; the paper was still moist.

Salix hippophaëfolia.—Branch 1 inch thick; bark slit up as in the preceding, but the fluid was actually dropped in on the 18th and 19th of June. On the 20th it was found that the solution had not gone beyond; even the layer of sap-wood was scarcely penetrated ⅛th of a line deep.

Salix arbuscula.—Branch $1\frac{1}{4}$ inch in diameter. Repeatedly wetted, as in the preceding case, during eight days: result almost the same. The solution had only advanced 1 line beyond the exposed spot, and quite uniformly upwards, downwards, and to the side; the sap-wood reacted $\frac{1}{4}$ of a line deep. When the experiment was continued for eighteen days the result was the same.

Consequently there is no layer in the whole tree less favourable than the cambium for the conduction of the sap. In opposition to the views of many inquirers, this part, being in the most active condition of development, most energetically arrests the fluids.

It is clear how unfitted the bark is for the transport of fluids; they occupy a longer time there than in most other parts, in changing their place. And in this experiment, we must not be led away by the results of what are called the "magic rings*" on trees. For if a thickened border is formed on them at the upper cut edge, this only proves that the sap in general has a descending motion; not, however, that this *does not take place far better and more easily in the totally uninjured woody layer.* When we reflect that even in the oldest trees a continual incrustation of the cells, a continual increase of that transformation of the saps, goes on deep in the interior of the wood, the result of which is the concentric growth of the *heart-wood*, at the expense of what is at first sap-wood, it is seen at once that it would be a great mistake to regard the wood, on account of its solidity, as lifeless and unengaged in the conduction of the sap.

3. *The Descending Sap in absorption by the* ROOT.

Salix alba, L.—A piece $1\frac{1}{2}$ foot long, of a shoot $\frac{1}{2}$ an inch thick, was placed in the ground on the 24th of February, and kept at a moderate temperature, so that roots were formed, and by the 20th of April leaves had already burst out. On the 6th of June the rooted portion was carefully split up the middle, from below upwards, and one of the halves immersed in solution of the ferrocyanide, the other in a vessel of pure water standing close beside. On the 14th all the leaves were dead, the roots still fresh and healthy. On the 4th of July the height of the fluids in the two vessels was not perceptibly altered, whether the levels were previously alike or different, as counter-experiments

* Made by removing a ring of bark running all round the tree.

proved; therefore no siphon action had been exerted. On this day the twig was analysed. The solution had not only ascended to the upper end in the one part, but also *descended* in the other part (at the water side), and indeed just to the surface of the water; it had penetrated farthest of all in the vascular part of the outermost *wood*, which, at the upper part, was in contact with the absorbing half of the shoot; in the liber and bark it fell about 1 inch short of this, while the inner wood, the medullary rays, and the pith, did not react. The surrounding water exhibited no reaction, which, it may be remarked in passing, does not speak much in favour of the hypothetical "root-secretion." The half dipping in the saline solution, when examined upwards, reacted most in the medullary sheath, and in the (two) outer layers of wood; also, however, in the liber and bark; while the inner (third) layer of wood and the pith had not conducted so far. At the upper free and undivided extremity, the branch reacted only at one side, that corresponding to the vessel containing the saline solution; therefore the solution had not passed round by the top to descend into the other half (to the water), but had gone over (in extremely small quantity) horizontally from wood to wood further down.

When the experiment was stopped sooner, in other cases, it was found (June 12th) that the solution had merely ascended, and not descended; in another piece of a shoot, the solution had descended half way in the water-half by the 15th of June. In one case, when the experiment was kept in action longer, the solution had descended $\frac{1}{2}$ an inch down below the level of the water in the half dipping in the latter,—not, however, to the highest of the little roots; here also the water exhibited no reaction; in fact, the portion of the inner layer of wood here laid bare by splitting the shoot had *not* conducted.

Whether, in these cases, the absorption of the saline solution took place through the roots, or also through the lowest exposed portion of the inner layer of wood, it is certain that here again the liber and bark were decidedly less concerned than the tracheæ of the wood, in the descent of the sap. It is seen that the descending sap, when it ascended from the *roots* and penetrated horizontally from wood to wood, avoided the *medullary sheath*, while it was shown in previous experiments that it very readily

passes into the latter when it is brought into the plant by the *leaves*; a circumstance which is doubtless to be explained by the intimate anatomical connexion between the vessels of the medullary sheath and those of the petioles in young shoots.

4. *The Descending Sap after direct absorption by* CUT SURFACES OF THE WOOD.

Salix vitellina.—The end of a pendent young leafy shoot was cut off, and the lower peripherical portion stripped of bark for 2 inches; the part thus laid bare was immersed 1 inch in the solution. At 2 inches further up in the same shoot, the bark was slit up at the side, and the cylinder of wood cut out for a length of 2 lines; the bark being returned to its place, and the wound wrapped in fresh leaves, the whole shoot was supported by a splint, to keep it in a fixed position. After four days the shoot had absorbed the fluid as far as it dipped in it. In this case the saline solution had *passed the bridge of bark*, had advanced $4\frac{1}{2}$ inches beyond the vacancy in the wood, and into *all* parts; furthest, however, in the bark and wood, principally in the medullary sheath and the peripherical part of the wood. Repeated experiments gave the same result, but sometimes the liber, sometimes the wood, had conducted a little farther. Consequently, here, where a forced entrance of the fluid had accomplished the passage through the bridge of bark, the solution had again penetrated in the horizontal direction through the wood above this bridge, and sometimes even advanced further in it than in the bark itself.

S. alba.—A portion $1\frac{1}{2}$ foot long of a leafy young shoot was stripped of its bark for 2 inches at the upper end, and dipped, with its wood wrong end upward, 1 inch deep in the solution. Then 1 inch of bark was peeled from the other free end, and a closed glass tube turned down over it to prevent desiccation. After seven days the fluid had ascended through all parts; whence, comparing this with the cases mentioned in section A 2, it results, that in absorption by exposed layers of wood, *it makes no difference* in the conduction of the sap whether the *shoot* is immersed in the fluid *upright or in a reversed position*. In this case also, some salt had crystallized out upon the leaves. When the free end of the wood was enveloped in blot-

ting paper, the latter absorbed a great deal of the solution (in the horizontal direction from the wood) even when the bark much lower down was unaffected. Or if only a ring of bark was cut out on the upper part of the shoot, this interruption was no hindrance to the advance of the solution; it was found at the end, both in the wood and in the bark. The epidermis did not give a blue reaction even after remaining one hour in contact with the salt of iron.

Salix acuminata, Sm.—The question investigated in this case was, how far a *horizontal* conduction of the fluids can take place under favourable circumstances in the *wood itself*, through layers of different ages. For this purpose the point of a small twig was cut off, at the end of June, and the open end immersed in the solution. The main shoot (6 lines thick) which bore the foregoing was so notched circularly in four different places, that there was no immediate communication with the vessels of the stem in any place: the wounds were enveloped in fresh leaves. After eight days it was found that the solution had advanced exclusively in that side of the main shoot which corresponded to the absorbing twig, and indeed only *as far as the notch* which interrupted the vascular communication 4 inches further up. Here also the outermost layer of wood and the liber had conducted principally, and not the cellular intermediate layer of the bark. From this we see what difficulties are opposed to the assumption of a horizontal movement of the sap through the medullary rays; although, at the same time, a horizontal movement of the saps in the young wood, *generally*, under very favourable circumstances, as in the experiments of Hales (*l. c.*), cannot be disputed.

Postscript.—With regard to the behaviour of the milk-sap, which I had an opportunity of observing in several *Euphorbiæ*, in *Sonchus oleraceus*, &c., in reference to the conduction of sap, I am led to assume, from all that I could notice, that it takes *no part whatever* in this, whether the fluid penetrate into the plant through the leaves or through the roots, setting aside all the anatomical reasons against a circulation of the milk-sap, the most decisive of which is, that in the majority of plants the milk-sap passages have no continuity or general distribution. [A.H.]

Article II.

Upon the Male of Argonauta Argo *and the* Hectocotyli. *By* Professor Heinrich Müller *of Würzburg.*

[From Siebold and Kölliker's *Zeitschrift für Zoologie*, June 1852.]

AMONG the many perplexities presented by the sexual relations of the Cephalopoda, we have had to reckon, even up to the present time, the statement of the majority of observers, that they had found none but female Argonauts. I believe that in the present essay I for the first time describe the perfect male Argonaut, as one of the arms of which the so-called *Hectocotylus Argonautæ* is developed. The *Hectocotyli*, which, from the first, Cuvier called "truly extraordinary" creatures, will none the less deserve that title.

It is well known that Kölliker* has endeavoured to show that the *Hectocotylus* of the Argonaut, described by Delle Chiaje† and afterwards by Costa ‡, is the male of this Cephalopod; that the newly discovered *Hectocotylus Tremoctopodis* also is the male of *Tremoctopus violaceus*, D. Ch.; and Von Siebold§ has assented to his views.

More lately Verany‖, in his work upon the Cephalopoda, communicated some very important discoveries with regard to the *Hectocotylus* of an Octopod. He found, that among five specimens of a peculiar species which he had previously named *Octopus Carena*, in three the third arm upon the right side was longer and stronger than the others, and was provided with a vesicle at its extremity. The fourth specimen had in the same position a short pedunculated vesicle; and the fifth possessed simply the peduncle without either arm or vesicle. Filippi noticed that the longer arm, which in one instance was observed

* Annals of Natural History, 1845. Linnæan Transactions, vol. xx. Bericht von d. Zootomischen Anstalt zu Würzburg, 1849.

† Descrizione, iii. p. 137, tab. 152.

‡ Annales d. Sciences Nat. 1841, p. 184 and pl. 13.

§ Vergleichende Anatomie, p. 363.

‖ Mollusques Méditerranéens, 1ère partie, Genoa, 1847–51.

to drop off on being touched, resembled the *Hectocotylus Octopodis* of Cuvier*, and Verany concludes from thence that this *Hectocotylus Octopodis* is a deciduous arm bearing male organs which are probably periodically developed. With regard to the *Hectocotyli* of the Argonaut and of *Tremoctopus* on the other hand, Verany believes that they cannot be arms of the corresponding Cephalopoda.

These statements rendered the subject of the *Hectocotyli* far more difficult than ever. It could hardly be believed that the *Hectocotylus* of the *Octopus* could be really distinct in its nature from the two examined by Kölliker; and yet upon the other hand, there were many reasons for hesitating to apply the conclusions drawn from the former to the latter. The *Hectocotylus octopodis* differs in many respects from the others; its sexual relations are less certain, while those of the Octopods to which it was attached, either in the mantle or as an arm, are wholly unknown; and finally, the positive assertions of Madame Power and Maravigno (see Kölliker, *l. c.*) seemed to prove that the *Hectocotylus Argonautæ* was developed as such in the ova of the Argonaut.

While at Messina, in the past autumn, I was very desirous of repeating the observations of Madame Power; but notwithstanding the examination of many thousand ova of all the Argonauts which I could procure, I merely found embryos of the ordinary form more or less developed; never those vermiform young, whose description had led to the belief that the *Hectocotyli* were developed in especial bunches of ova.

At last, at the end of September and in the beginning of October, there were brought to me, among many very small Argonauts which had not yet acquired a shell, a few of a quite peculiar form. Their cephalic extremity presented a little sac, which projected between the arms, as the animals swam about with their peculiar retrograde movement. On closer inspection† one could perceive seven arms, which all terminated in points like the six lower arms of other Argonauts of the same size. The

* Annales d. Sc. Nat. 1829, p. 147, pl. 11.

† The relations of the parts were clearest when the animals fixed themselves during life, within a glass, so that one could look from without straight down upon the oval surface of the head; or after death, by placing them in a waxen pit so as to obtain a similar view.

two upper and the two lower arms were longer than the lateral ones; of the latter on the right side three only were present; while on the left side there existed, in all the specimens which I received, in the place of the lower lateral arm, the sac in question, supported by a short and delicate pedicle, as if it were constricted. The pedicle arose from a small depression between the second and fourth arms and the mouth, from which the sac could be easily drawn out a little. The membrane which unites the base of the arms of the Argonaut passed upon the left side from the second to the fourth arm, without immediately investing the sac, whose position was somewhat internal to it.

The sac itself was not so long as the arms in the smallest specimens, whilst in the larger it equalled or exceeded them in length. In shape it was not exactly round, but somewhat elongated and compressed in such a manner that the diameter in a radial direction from the mouth was greater than in the line of the two neighbouring arms. The colour, like that of the rest of the body, was intensely reddish brown when the chromatophora were dilated, more greyish when they were contracted. Only on the inner, oral side was there a white streak without chromatophora, which however did not extend over the whole length of the sac.

In all cases a Hectocotylus Argonautæ *lay coiled up within the sac.* It was curved towards the side which bears the suckers, so that the back of the thick part corresponded longitudinally with the internal convexity of the sac. The part described by Kölliker as a silvery sac, forms at this place, immediately under the skin of the sac in large specimens, a ridge-like elevation visible externally, through which a whitish tint often glistens. The thinner part of the sucker-bearing body is bent back along the inner convexity of the sac towards the base, and the filiform appendage lies between them in multitudinous convolutions.

This position of the *Hectocotylus* is frequently obvious from without, especially during the lively movements which it often makes; and still more clearly on the opening of the sac, when it uncoils itself from its narrow cell under the eye of the spectator.

The relation of the *Hectocotylus* to the capsule in which it lies, and the change which the latter undergoes after its eversion, are very remarkable.

I may here observe, that in one case the sac burst before my eyes, along the inner, oral side, in consequence of the violent movements of the *Hectocotylus*, when the process about to be described took place in exactly the same manner as in other specimens which were artificially opened.

It is observed, in the first place, that the thick end of the *Hectocotylus* is fixed to the pedicle of the sac or forms it; next, that the membrane of the sac is perfectly distinct from the filiform appendage and from the neighbouring parts of the sucker-bearing body; but that, upon the thick portion of the body, while it leaves the sucker-side free, it is attached along the back behind the suckers, and forms the covering of the silvery sac above mentioned.

The so-called pigmented testis capsule of Kölliker, however (as it is observed in the *Hectocotyli* which are found free upon female Argonauts), does not yet exist, and is subsequently formed from the membrane of the sac.

As soon indeed as the appendage and the thinner part of the body, which usually become twisted upon their axis at the same time, are evolved, the thick part bends forcibly back in the opposite direction to the previous curvature, that is towards the back. By this means the longitudinally cleft membrane of the sac is inverted, so that its inner surface comes to be exterior, and the edges of the torn part are turned back towards the back of the *Hectocotylus*, which is now concave. The previously external pigmented layer of the sac now lies in the pit between these edges, and when the latter have united, there is left only a small cleft, a process which can naturally not be directly traced. We have just such a pigmented capsule formed as has been already found in the dorsal crest of *Hectocotylus Argonautæ*.

In this way we readily account for the singular fact, that a colourless layer is constantly found upon the exterior of the dorsal crest, while the layer of chromatophora lies internally upon the so-called capsule of the testis.

The membrane of the sac then belongs to the future *Hectocotylus*. This was seen most clearly in that specimen in which, as has been already noticed, the sac opened spontaneously; for upon touching the *Hectocotylus* frequently it detached itself from its delicate pedicle so as to carry away the inverted sac with it.

However, as the cleft in the sac had not extended quite so far as the insertion of the pedicle, the first suckers still remained hidden by the pigmented sac, whose borders began to be reverted only opposite to the fourth sucker.

The case here cited hardly allows us to doubt that the *Hectocotylus* once formed is intended to become detached from the rest of the animal; as might indeed already be concluded from the fact that all the *Hectocotyli* seen by Delle Chiaje, Costa and Kölliker, to which I can add thirteen others, were found separated and associated with female Argonauts. Hence also it would seem to be probable that the detachment of the *Hectocotylus* is preceded by the bursting of the sac; though I have found no specimen in which when captured the *Hectocotylus* had already made its exit from the sac. When and in what manner the separation of the *Hectocotylus*, and its transport to the female, go on; whether any act of copulation, for instance, takes place, were points upon which I had no opportunity of making any observations.

I will now first consider a few points with regard to the external and internal structure of *Hectocotylus Argonautæ*; and I will then compare the *Hectocotyli* of *Octopus* and *Tremoctopus* with it. For the most part I have only to confirm Kölliker's observations, though of course my interpretation of them must be somewhat different. The name "*Hectocotylus*" may very well be retained, without any implication of independent animality.

Hectocotylus Argonautæ.

As to external form, there were two portions to be distinguished in all the *Hectocotyli*, whether free or enclosed in sacs, which I examined: the one thick, and carrying suckers; the other called by Kölliker the filiform appendage, thin and suckerless, but directly continuous with the former.

In the free *Hectocotyli* the body and its appendage sometimes attained the length of an inch or more each; in other cases, each was some lines shorter. A few of the *Hectocotyli* which were just set free from the sac had this latter size. In three specimens, in which the body and head of the whole animal, as far as the base of the arms, were about 4 lines long, the sucker-bearing portion of the *Hectocotylus*-arm measured 8–10 lines, and

the appendage about as much more. In an animal of 3 lines long, each part of the *Hectocotylus*-arm was a few lines shorter. The smallest specimen which I met with measured 2 lines to the base of the arms; body and appendage of the *Hectocotylus*-arm each 3–4 lines. The length of the uninjured sac was about 1 line in an animal of $2\frac{1}{2}$ lines; on the other hand, it was 3 lines in a specimen whose body, as far as the arms, was 4 lines long*.

At the thick end of the detached *Hectocotyli* is the point, where the constricted axis must finally have divided; it is drawn a little towards the dorsal side, while the first suckers project somewhat forward. No trace of any rent is to be seen, but the surface is quite smooth as if cicatrized, and the fringe which unites the suckers upon their dorsal side is also present between the oblique anterior pair, so that the one series of suckers passes in a continuous curve into the other.

The point of transition of the thicker body into the filiform appendage is sharply marked in all the free *Hectocotyli* and in the larger enclosed ones. The suckers with the fringe which unites them cease suddenly, the axis of the body becoming thinner and passing into the appendage. In the smallest specimen before mentioned, on the other hand, the transition was far more gradual. The suckers in the posterior broad part of the body, which did not measure more than ·15 of a line across, became gradually smaller and more rudimentary, and finally appeared as mere transverse elevations; when they ceased the diameter of the body was still 0·1 of a line.

The membranous lobes described by Kölliker at the origin of the suckerless part of the body were present in all free *Hectocotyli*; but it could generally be clearly observed that there is properly speaking only a single lobe, which in its highest part crosses the body of the appendage transversely, and then passes gradually upon each side into a slight fold. These two folds run along the appendage for a considerable distance: in one case, the most elevated portion of the lobe was prolonged into two elongated processes. The height of the transverse portion

* An eighth specimen, in which both the body and the unopened sac surpass the above dimensions, is in the possession of M. Verany, who immediately recollected it on seeing my specimens. It had previously been brought by Krohn from Messina.

varied from an inch to more than half an inch (1 *bis über* $\frac{1}{2}''$). The fibrous tissue of which the lobe consists is contractile, and frequently moves very vivaciously by itself. In the yet attached *Hectocotyli* the lobe was in the same way more or less developed, and was wanting only in the smallest specimen. This is unfavourable to the view that the lobe is a residue of the torn sac; which might otherwise suggest itself, especially since the strong resistant epithelium which externally coats the appendage is absent upon the lobe. The edges of the lobe were generally smooth and did not appear torn.

Of the tentacular cirrhi which Costa (*l. c.* fig. 2^{a} *e* and *f*) depicts at the anterior end of the *Hectocotylus*, I could never find any trace, and I am inclined to believe that they were some accidentally adhering foreign bodies, since nothing could be lost or torn away, in the *Hectocotyli* otherwise perfect, which were taken out of the sac.

Such specimens as the latter are also important for the determination of the interpretation which is to be put upon the dorsal pigmented capsule * and the position of the appendix in it. Kölliker has called this capsule the capsule of the testis;—inasmuch as in one specimen he saw the filiform appendage enter it through a cleft in the back, and become connected therein with a coil of seminal canals, to which he gave the name of 'testis.' I believe that the presence of semen there is accidental, and that another interpretation must be given to the position of the appendage. It has been already stated, that there exists no capsule in the *Hectocotyli* while still included in the sac; the appendage is always free, and nothing is to be seen of any seminal canals. In the free *Hectocotyli* the capsule was indeed always formed, but in many instances it was quite empty, the appendage also lying outside it. In other cases the appendage passed, in the manner depicted by Kölliker (pl. 1. fig. 9 and pl. 2. fig. 17), through the cleft of the dorsal ridge into the pigmented capsule, but lay free therein, no seminal canals being present.

* The chromatophora here exhibit in free *Hectocotyli* the same movements as elsewhere. The radial muscular fibres are clearly recognizable, contracted or relaxed according as the chromatophora appear large or small. Muscular fibres are also found in the deeper layers of the cutis in *Hectocotyli* as elsewhere among the Cephalopoda, *e. g.* in the dorsal ridge.

This could be seen partly upon opening the capsule, partly from without during the movements of the *Hectocotylus*. The appendage not only twisted about in the capsule, but crept alternately out and in, so that even the thin part of the sucker-bearing body, as far as it would go, became hidden in the capsule. The *Hectocotylus* then crawled about in a very peculiar manner with this inserted part, which formed about the middle of the body, directed forwards. On the other hand, if the *Hectocotylus* were disturbed by touching, it not unfrequently drew its appendage quite out of the capsule, and could then be no longer distinguished from the first form which has been mentioned.

It appears then, that the appendage makes the pigmented capsule its residence either from being accustomed to its previous imprisonment in the sac, or as a sort of presentiment of its proper position *.

The exceptional occurrence of seminal canals in the capsule of Kölliker's *Hectocotylus* is explained, if we consider the route which the semen must take to be poured out.

Kölliker has exactly described the course of the vas deferens between an aperture in the neighbourhood of the point of the appendage and a thick silvery sac which lies under the pigment-capsule. He called that sac a penis, or finally, vesicula seminalis; assuming that the semen passes out of the capsule (testis) along the appendage, then into the ductus deferens along the back, and finally out of the silvery sac at the thick end of the *Hectocotylus*.

However, in the most free *Hectocotyli*, and even in the largest of the included ones, we find this sac completely filled with semen. Sometimes this distension extends into the ductus deferens to a greater or less extent, and evidences itself to the naked eye even, by an intense white streak along the back and appendage of the *Hectocotylus*. Lastly, on one occasion a *Hectocotylus* passed a whole coil of a thread, about ·06 of a line thick and consisting of spermatozoa, from the aperture of the appendage, and the thread remained attached to it, so that the appear-

* Considering the occurrence of gills in *Hectocotylus Tremoctopodis*, we might ask whether that form developes a digestive organ, for which Cuvier took the capsule in *H. Octopodis*. At present however we have no evidence upon the point.

ance figured by Kölliker (pl. 2. fig. 19) arose: only the appendage was free, while in Kölliker's specimen it was inserted in the pigmented capsule.

We may hence assume that the semen during ejaculation passes from the thicker sac towards the point of the appendage*. It agrees very well with this conclusion, that a copulation very probably takes place during which the appendage represents the penis (*vide infra*). Kölliker's *Hectocotylus* therefore only committed an *error loci* when it deposited its semen in the pigmented capsule. The presence of an investment to the seminal coil which Kölliker found in the pigment-capsule, is not, as I believed at first, any argument against its secondary deposition there, for a structureless layer was also very visible in the free seminal cylinder, at least in some portions of it. It is perhaps only analogous to the structureless mass which is to be found elsewhere in the sexual canals of the Cephalopoda, and is deposited around the semen when excreted. In a second instance I could find no such investment.

Since the pigmented capsule upon the back of the *Hectocotylus* could not be the testis, the latter was to be sought for elsewhere. At first, I was tempted to consider the silvery sac as its representative; since not only was this full of perfect spermatozoa in all free *Hectocotyli*, but also in that *Hectocotylus*-arm already referred to which had burst its sac after its spontaneous detachment. Nevertheless it was surprising that in other *Hectocotylus*-arms just taken out of their sac, the silvery capsule had not its white colour, and neither perfect semen nor any stages of its development were to be perceived therein.

Subsequently I convinced myself that there is unquestionably a testis in the abdomen of the animal which carries the *Hectocotylus* as an arm. Behind the gills and venous appendages a great part of the mantle-cavity is taken up by a capsule, whose free lower wall is very remarkable on account of its isolated chromatophora scattered over as hining golden ground. Behind,

* In most cases I could not exactly make out the place of the aperture, though in the two upper thirds of the appendage the ductus deferens is usually easily recognizable, and even far forward has a diameter of 0·05 of a line when it is not collapsed. On one occasion I succeeded in pressing the semen from the silvery sac to within two lines of the point where the ductus deferens only measured 0·03 of a line.

it adheres to the mantle. In the capsule lies a white mass which consists of little cylinders or cæca which are united at one extremity: their length is about 1 line, their thickness 0·06–·1 of a line. A clearly-defined tunica propria could not be distinctly recognized in these spirit specimens for each cylinder, but expanded membranous coverings could be frequently observed between them. In the cylinders themselves large pale cells lay at the periphery; the interior was in one case occupied by masses which consisted of numerous granules of about 0·002 of a line in diameter, and which had frequently a delicate process in an oblique direction with regard to the axis of the cylinder. In a second specimen there could be no doubt that these lumps were forms of the development of the spermatozoa. There lay in the same position more or less developed bundles of spermatozoa, whose somewhat wavy threads had the same oblique direction with regard to the axis of the little cylinder. This appeared, consequently, to be quite a fibrous streak. The length of the single bundles was about 0·08 of a line.

In these two animals provided with full testes, the generally white and distended capsule of the *Hectocotylus* was colourless and collapsed. In a third animal again, which had carried the detached *Hectocotylus*-arm filled with spermatozoa, the shining golden capsule was indeed present, but it was empty. If we connect all these facts together, it becomes very probable that the semen is produced in the testis, and that it is then transferred into the *Hectocotylus*, although I could not recognise with certainty this portion of the ductus deferens, which must lie under the skin of the head.

The silvery capsule, then, would be neither penis nor testis, but vesicula seminalis; and so long as the *Hectocotylus* remains connected with the rest of the animal, the essential distinction from other cephalopod males must consist in this, that the aperture of the ductus deferens, instead of lying in the mantle-cavity, is placed at the end of the peculiarly-developed arm.

The structure of the silvery capsule harmonizes very well with this interpretation. It is, as Kölliker has shown, very muscular *, and in its interior there lay in all the free, and in the largest of the

* The muscular fibres are distinguished from those of the rest of the body by a peculiar development, a point to which I shall recur elsewhere.

included *Hectocotyli*, the coils of a thread of 0·06–0·08 of a line in diameter, consisting of perfect spermatozoa. I have not seen the aperture of this organ, stated to exist by Kölliker at the extremity of the thick end of the *Hectocotylus*. If the semen be actually passed out of the testis into the capsule, such an opening must exist at one period or other; but it probably becomes closed behind the deposited semen before the detachment of the *Hectocotylus* takes place.

The spermatozoa of the Argonaut consist of a very delicate thread, at one of whose ends is a somewhat thicker fusiform body. They are therefore analogous to those of *Tremoctopus*, but smaller, since they measure, as we see especially in the bundles, only 0·08–0·09 of a line in length, of which we may consider the body to form 0·01 of a line. In general the bodies lie grouped together, and from them the threads pass nearly parallel, like the cilia of a colossal ciliated epithelium. On one occasion almost every bundle of bodies was spirally twisted. This occurred in the appendage of a *Hectocotylus* which I found in the ovarian capsule of a female Argonaut. In this one case I saw a lively movement in the spermatozoa, the groups of which formed regular progressive waves like the sea after a strong breeze.

What is there in the muscular tube which forms the axis of the Hectocotylus? is a most important question.

Since we know that the *Hectocotylus* is developed as an arm, it may be surmised, *à priori*, that the structure of the whole axis will nearly resemble that of other arms, as indeed Kölliker has already shown it does, so far as the muscular tube is concerned. In fact, there lies in its interior a chain of ganglia, which answer to the suckers. We see them best in longitudinal sections which have been placed in solutions of chromic acid or corrosive sublimate, and the single ganglia may be separated and demonstrated as far as the root of the filiform appendage. From this point the muscular tube may be very readily traced to the extreme end, but it is difficult to make out what it contains: certainly not the vas deferens; for this, as Kölliker has shown, is only attached superficially. In fresh specimens I saw a few times a clear tube-like streak, which gave off lateral branches as well in the axis of the sucker-bearing portion as in that of the

appendage, in which it measured only ·012 of a line; but of its nature I can say nothing. The thickness of the whole axis measured in one case at the end of the seminal capsule 0·39 of a line; towards the end of the sucker-bearing portion 0·3 of a line; in the beginning of the appendage 0·15 of a line; at the end of it 0·03 of a line. The inner tube measured at the same points 0·24, 0·18, 0·08, and 0·025 of a line.

The development of the *Hectocotylus* as an arm, while it explains the presence of a ganglionic chain, equally accounts for the absence of any special organs of sense. But on this ground the sensibility of the skin is very considerable.

Since the muscular tube is filled by the chain of ganglia, the supposition that an intestinal canal exists there, which Kölliker himself considered doubtful, must be given up; at least I have perceived nothing of the kind.

With respect to the circulation, I can unfortunately give no information as to the connexion existing between the *Hectocotylus* and the rest of the animal. In the separate *Hectocotyli* the investigation is beset with difficulties, since they are for the most part very restless, and wind and twist about in the most determined manner. Yet a progressive wavy motion can readily be observed in the trunks which lie upon each side of the back and are immediately continued into the appendage. In one instance I could distinctly perceive that this somewhat slow movement passed upon the right side (the appendage being supposed to be posterior and the suckers below) as far as the extreme point of the appendage, and then returned in the opposite direction.

After each wave towards the point, however, there succeeded not merely a centripetal one upon the other side, but centripetal movements frequently arose, which commenced from the point of the appendage. In other cases I met with a different rhythm in the longitudinal trunks of the one and of the other side, and a few times it appeared to me as if in the same vessel the movement went on sometimes in one sometimes in the other direction, as in the Tunicata. However, two vessels lying close together might readily cause a deception in this case.

Whether any distinct central organ of the circulation or heart exist, I cannot as yet decide.

There occur indeed considerable dilatations in the vessels;

especially in one specimen, in which I found after the circulation had ceased, a sacculated space ·15 of a line long by ·018–·08 broad in one of the longitudinal vessels of the back, somewhat behind the extremity of the seminal capsule. At both ends of the dilated portion more delicate lateral branches were given off. Somewhat further behind upon the same vessel, and in a corresponding position upon that of the other side, there was a rounded expansion of ·05–·06 of a line in diameter. If these dilatations are to be called hearts—in which case they might be considered to undergo a further development—we must suppose that such exist in many places, which would agree with the general arrangement in the Cephalopoda.

But it may well be that these spots had merely remained accidentally dilated after death, for the narrower parts of the vessels were evidently contracted, and one of them, further on in the thick part of the body, was evenly dilated to 0·05 of a line. The differences in breadth, which may be successively observed in the same place during life, are again very considerable. A vessel between the axis and the seminal capsule measured in its condition of expansion 0·05 of a line, and contracted to ·02 of a line.

This rhythmical expansion and contraction of the larger vessels goes on in somewhat different modes. Frequently one portion of a vessel is suddenly distended by the wave propelled by the contraction of that portion which lies immediately behind it, and then collapses again. At other times one part is slowly distended by the blood which streams in gradually, especially out of the smaller vessels, and at last contracts with a jerk, whereby the vessel in consequence of its elongation becomes much bent.

The independent share of single portions of the vascular system in the centripetal movements of the blood is very clear here as in other parts of the Cephalopoda, *e. g.* the gills.

More or less rhythmical and swift contractions are seen to drive the blood from the smallest venous twigs into the larger trunks; these help it on further either by an immediate contraction, which is a continuation of that of the smaller branches, or only after they are more dilated by the repeated contractions of the latter. That this venous movement is nowise propagated from the arteries, is clear from the circumstance that single

ramifications often pulsate rapidly, while the neighbouring ones are either still or move at a different pace. These relations are especially recognizable in those ramifications which come off from a transverse branch of the longitudinal trunks, between every pair of suckers, and spread in the membranous fringe connecting these.

Here, as in many other places in the Cephalopods, one may readily convince oneself of the existence of capillary vessels.

Concerning the development of the male Argonaut I can state nothing, since I unfortunately obtained no more ova advanced in development, after I had discovered the *Hectocotylus* to be an arm; and inasmuch as I had not previously paid sufficient attention to the form of the arms, in the expectation of finding the totally different vermiform embryos described by Madame Power. Indubitably, however, the male embryos are not to be found in especial bunches of ova, but have been frequently seen among the female ones by Kölliker and myself, although from the similarity of their form no further notice has been taken of them. One is the more justified in this supposition, since the sac with the *Hectocotylus* appears to be relatively smaller the younger the animal, and from its shape might be easily confounded with the yelk-sac.

In some preserved ova of the Argonaut far advanced in development, I believe that I can recognize the arm of the *Hectocotylus*.

The statements of Madame Power and of Maravigno quoted by Kölliker (*l. c.* p. 84) contain truth and fiction; but they may be thus interpreted. What are denominated *Hectocotyli* three days old are without doubt *Hectocotyli*; the description of them which is given, no less than the statement that only two or three are developed in the maternal shell, accords very well with this view. For if we procure Argonauts with advanced ova, in a short time we see the hatched young swim about in innumerable multitudes. The statement that the seven other arms spring out as buds from the vermiform animal while it is assuming the form of the common Argonaut, leads one almost to believe that Madame Power saw entire male Argonauts with *Hectocotylus*-arms everted from their sacs in the shell of the female Argonaut.

If this were demonstrable from the original manuscript, it would afford an important evidence in favour of the immediate transportation of the *Hectocotylus* from the whole male upon the female Argonaut.

In the following pages I will bring forward for comparison all that is to be said concerning the two other known kinds of *Hectocotylus*, for it is precisely the very striking differences and similarities of the three *Hectocotyli* with one another, that promise in course of time to afford an insight into the meaning of the separate organs and the nature of this singular creature as a whole.

For this purpose I refer to the description by Kölliker of the *Hectocotylus Tremoctopodis*, and to that of the *Hectocotylus Octopodis* by Cuvier and Verany. Although the identity of the species of *Octopus*, in which Cuvier and Verany found their *Hectocotyli*, is not demonstrated, yet the *Hectocotyli* are so nearly related that they may well be considered together.

Hectocotylus Octopodis.

As Kölliker has shown, the *Hectocotylus* of the *Octopus* is distinguished from that of the Argonaut not only by its greater size, but because at one extremity instead of the filiform appendage there is a vesicle containing a filament; in other respects the two forms essentially agree.

Upon comparing the figures of Cuvier and Verany, we find that the "solid cylindrical body" which Cuvier indicates as the origin of the silky thread is the muscular axis; the supposed nervous threads of Cuvier are the vascular trunks, which in *Hectocotylus Argonautæ* take on a similar appearance in spirit; the sac (*e*) filled with the coils of a white thread is the thicker seminal capsule; the canal (*h*) is the ductus deferens upon the back; the "stomach" (*d*) corresponds with the pigmented dorsal capsule of *Hectocotylus Argonautæ*. The position of the aperture of this capsule alone differs, since in *Hectocotylus Argonautæ* it remains at the posterior end, while Cuvier has depicted it at the anterior (*f*). According to this figure and Cuvier's statement that this opening (which he calls a mouth) in the fresh state is slit-like and leads into the pigmented capsule, as well as from the analogy of *Hectocotylus Argonautæ*, I cannot agree

with Kölliker (pp. 79 & 80) that this aperture belongs to the seminal capsule. Whether a second aperture for this exists at the anterior end is not certainly determined by Cuvier himself, and he does not state that Laurillard had seen the semen poured out anteriorly. The connexion which, according to Cuvier, exists between the thread (*i*) everted from the terminal vesicle, on the one hand with the axis of the body, and on the other with the canal (*h*), which, coming from the seminal capsule, is evidently analogous to the ductus deferens in the Argonaut, is singular.

If with Kölliker we may be permitted here to suppose an error on the part of Cuvier, who only examined spirit specimens, I should imagine, keeping in view the fact that Verany found a filament with a free and pointed end in the terminal vesicle of the *Octopus*, that the latter was overlooked by Cuvier. If this be the case, the analogy between the filament exserted from its vesicle and the filamentous appendage (penis) of *Hectocotylus Argonautæ* becomes striking.

It would then require to be made out whether and how this appendage makes its exit from its vesicle, and we might conceive similar relations to those which I shall subsequently show obtain in *Hectocotylus Tremoctopodis*. In the latter case the presumed error of Cuvier would be easily explicable. The above-mentioned differences in the position of the pigmented sac might also be connected with the difference in the position of the appendage, since in *Hectocotylus Octopodis* the supposed appendage is perhaps never meant to pass into that pigmented capsule as in *Hectocotylus Argonautæ*.

From the structure of the *Hectocotylus Octopodis*, especially the presence of the silky thread in the capsule, *e*, and the assertion of Dujardin (*Helminthes*, p. 131) that the white thread consists of spermatozoa, the male nature of this *Hectocotylus* also may be concluded.

Its development is probably quite similar to that of the *Hectocotylus* of the Argonaut.

Verany and Filippi (see above) have already proved that the *Hectocotylus* of the Octopod arises as one of its arms. Verany has observed in the same place a sac, which, according to the figure in which chromatophora are indicated, appears rather to be analogous to the sac of the male Argonaut than to the

vesicle which otherwise terminates the *Hectocotylus Octopodis*. The pigmented capsule upon the back of the latter again is evidence of a process of eversion similar to that of the Argonaut; and in the specimen of *Octopus*, which M. Verany had the goodness to show me, the pigmented spot upon the back of the *Hectocotylus*-arm appeared very similar, if I do not err, to that upon the back of the *Hectocotylus*-arm of the Argonaut when just everted from its sac. Here also then the eversion of the *Hectocotylus* from its sac precedes its separation. Whether the pigmented capsule is already developed in one of Verany's specimens I know not. It is interesting that Cuvier describes one of his *Hectocotyli* as the arm of the *Octopus*. Four out of five individuals were found in the mantle of the Octopod; "the fifth had attached itself to one arm of the Poulpe, and had changed it into a kind of sac in which it had imbedded its head, whilst the rest of the body remained free externally (p. 150);" and "it has almost destroyed the arm, and appears to replace it so completely that at first it might be taken for the arm itself" (p. 149). It is hardly to be doubted that the animal "qu'un parasite dévore" was a male *Octopus*, which carried a *Hectocotylus* newly freed from its sac, but not yet separated. The last link of the series finally is formed by that *Octopus*, in which Verany found merely a short stump in the place of the *Hectocotylus*-arm, which in all probability had already fallen off.

Considering the general resemblance of the *Hectocotyli* of the Argonaut and of the *Octopus*, it is very remarkable, that, according to Verany, in all cases the third arm of the *right* side is the abnormally developed one in *Octopus*, whilst in the Argonauts it always is the third arm of the *left* side. Cuvier does not state in the place of what arm his *Hectocotylus* was fixed.

It is much to be regretted that Cuvier has given no information as to the sexual organs of the Octopods which carried the *Hectocotyli* in their mantle or as an arm, and it is the more desirable that such Octopods should be closely examined, since their more considerable size will without doubt allow a more easy and better determination of many points than the small Argonauts permit.

Hectocotylus Tremoctopodis.

The third kind, the *Hectocotylus Tremoctopodis*, is intermediate in size between the two others; in form, however, it differs far more from the *Hectocotylus* of the Argonaut than from that of the *Octopus*. Nothing is known of its development.

However, besides the structure of the muscular tube of the body already pointed out by Kölliker, that of the suckers, and the presence of genuine chromatophora, we have one very important point of resemblance with the *Hectocotylus Argonautæ* in the presence of a longitudinal series of ganglia.

This ganglionic chain, which has already been recognized by Von Siebold, passes from the anterior end of the *Hectocotylus* to the commencement of the capsule in the abdomen. The single ganglia are so disposed that one lies upon each of the alternating suckers; they are thence closely appressed. If we make a longitudinal section, not perpendicularly between the suckers, but horizontally, we obtain precisely the view given by Kölliker, pl. 2. fig. 14. It is therefore obvious that the conical masses of granular substance described by him, at p. 74, were these ganglia.

The doubts as to the presence of any intestine expressed by Kölliker are quite just in this case. The opening which he also gives as doubtful, at the anterior extremity of the body somewhat towards the back, was perhaps only the end of the axis whose already attenuated tube here terminates—the inner layers contributing to form a blind end round the last ganglion, while the outer layers united with the skin form a more or less distinct knob*.

If in many cases an opening is actually present, this would indicate even more than the mode of termination which has been described, and which agrees with that of the thick end of the *Hectocotylus Argonautæ*, that supposing the *Hectocotylus* of the *Tremoctopus* to be developed as an arm like the others, this is its attached end.

The structure of the opposite end renders this conclusion

* Von Siebold also has concluded from the want of such an aperture that there is no digestive organ in *Hectocotylus Tremoctopodis*, and Cuvier affirms that in *Hectocotylus Octopodis* the axis has no opening anteriorly.

probable; the ovate or pyriform capsule in the abdomen being similar to that which in *Octopus* is certainly placed at the free end of the *Hectocotylus*-arm.

Besides, both in form and position that abdominal capsule is analogous to the membranous lobe on the appendage of *Hectocotylus Argonautæ*.

Among eighteen *Hectocotyli* of *Tremoctopus*, twelve had the abdomen constructed as Kölliker has described it. In six, however, the capsule of the abdomen had a cleft upon its dorsal side; this commenced close behind the last sucker of the left side (the suckers being supposed to be below and the capsule behind), and extended somewhat obliquely as far as the commencement of the delicate process into which the capsule is prolonged; the latter lay consequently wide open, and it could readily be seen that it was empty; that is, that it contained neither the convolutions of the seminal capsule nor the ductus deferens, which in other cases are found in the closed capsule*. Upon careful examination, however, the cleft is, even in all ordinary *Hectocotyli*, to be seen as a streak occupying the direction indicated. There is a ridge upon the right side; pale, more or less closely adherent, and capable of being raised. It can be observed then that the subjacent layer, upon the left side, passes for a certain distance under the other, and appears to be as it were rolled up at its anterior end.

In *Hectocotylus Tremoctopodis* this cleft then always exists, and it would be interesting to know whether it also occurs in the capsule of *Hectocotylus Octopodis*.

When the cleft is open and the capsule is empty and relaxed, it has a considerable resemblance in external character to the membranous lobe of *Hectocotylus Argonautæ*, which also at times forms a deep pit. Both organs exhibit a lively undulatory movement.

In order to comprehend more exactly the relative position of the capsule, it is previously necessary to show that the penis of

* I presume, that at least in most cases the capsule has been burst after the *Hectocotyli* were taken, by contact with fresh water or the like. In three *Hectocotyli* of the ordinary form which I had thrown into a dilute solution of chromic acid, I also found after a few days the capsule open and the contents fallen out.

the *Hectocotylus Tremoctopodis* is analogous to the filiform appendage of *Hectocotylus Argonautæ*.

Of the six specimens in which the cleft in the capsule was open, three were particularly distinguished by having no penis visible externally. It was not torn off, as might have been concluded from the absence of the opening out of which it generally passes*; but it lay spirally coiled up under the skin inferiorly behind the last suckers, and, indeed, more towards the right side. It was very short, but relatively thick. Here then it was clearly evident that the penis is the immediate continuation of the muscular axis, which could not be so well demonstrated in specimens with a long free penis. Close behind the last suckers, the end of the thick part of the axis, which contains the last ganglion, lies in such a manner in the lower wall of the capsule, that it can be seen through the dorsal cleft above mentioned as a knob somewhat projecting from the inner surface of the capsule. From this the muscular tube bends down to the lower side of the *Hectocotylus* and forms the penis, which here lies coiled up under the skin, instead of as usual passing forward and becoming free in the neighbourhood of the third to the fifth sucker.

Where the axis bends down, the longitudinal vascular trunks pass into the penis†. Immediately beyond this flexure the ductus deferens, generally convoluted, comes from the left side to the anterior side of the penis into which it penetrates. The larger convolutions which this duct frequently makes at the base of the penis produce the transverse ridge, which may be frequently observed in many *Hectocotyli* between the body and the capsule upon the lower side.

If now we consider the place of the cleft capsule, keeping in mind this relation of the penis to the axis, its position upon the back of the axis (where the thicker part passes into the thinner) is quite analogous to that of the membranous lobe in *Hectocotylus Argonautæ*.

* In one specimen the semicircular edge which usually surrounds the aperture behind was faintly indicated, perhaps in preparation for the subsequent exit.

† Whether at an earlier period the contents of the axis also are continued into the penis, I cannot decidedly say.

If then the abdominal capsule of *Hectocotylus Tremoctopodis* is analogous with this lobe, and perhaps also with the terminal vesicle of *Hectocotylus Octopodis*, we must give up its supposed analogy with the pigmented capsule of the two other *Hectocotyli*; and the *Hectocotylus Tremoctopodis* seems to possess nothing comparable therewith.

On the other hand, the presence of a free penis by no means constitutes an absolute difference from the other *Hectocotyli*. It is its position chiefly which distinguishes it from the appendage of *Hectocotylus Argonautæ*, and the circumstance that the ductus deferens lies in its interior, whilst in the latter it is only attached externally to the prolongation of the axis. If it were certain that the filament which we find in the terminal vesicle of *Hectocotylus Octopodis* had the same signification, and is not a mere seminal tube, the analogy of the three *Hectocotyli* in this point would be complete.

In the other portions of the sexual apparatus, the testis and the ductus deferens, such an agreement cannot at present be demonstrated.

Kölliker has named 'testis' a vesicle which generally completely fills the abdominal capsule. The cleft outer capsule readily separates again into two layers, the outer of which is similar to the general cutaneous investment: under the epithelium there is a fibrous network with numerous vessels, whose capillary loops may be seen in the delicate terminal prolongation. The second layer consists, like the subcutaneous tissue of the back, of muscular bundles, which especially affect a longitudinal arrangement. Upon the inner surface it supports a layer of delicate polygonal cells. Below this again comes the so-called sac of the testis, which may be easily separated. Its wall has a peculiar checkered (*carrirtes*) appearance; two layers of fibres are visible, which cover one another very regularly like the fibres of a tissue, at right angles, or often at somewhat oblique angles. The fibres are when isolated somewhat rigid, but oftentimes not dissimilar to muscular fibres. Elsewhere, however, they can be hardly separated at all, and in many places almost structureless layers occur.

In the interior of this vesicle there was always contained the thread described by Kölliker, which consists almost entirely

of perfect spermatozoa. In this case a special investment is frequently not to be discovered, as Kölliker and Von Siebold (*Vergl. Anat.* p. 411) state; in a few instances, however, the greater part of the thread was surrounded by a distinct structureless membrane.

Its existence was clear in places where it stretched over gaps in the contents, or where it was quite empty, and also in places where it was torn, and the masses of spermatozoa had swelled up and made their way out. Whether this investment is a true membrane which subsequently disappears, or whether more probably it is rather an accidentally deposited homogeneous mass, I will not attempt to decide; only it is to be noted that this investment was not to be found in a few other portions of the same seminal cylinder.

The one end of this filiform seminal mass is connected with the bulb which forms the commencement of the ductus deferens (ductus ejaculatorius, V. Siebold) described by Kölliker. One part of it lies coiled up with the seminal cylinder in the checkered vesicle, the other part stretches on into the penis.

This peculiar ductus deferens* appears to consist of a substance essentially identical throughout, but varying very greatly in consistence and form in different localities. It is a yellowish or colourless, sometimes tough, sometimes more brittle, but elastic mass, which frequently, *e. g.* in the interior of the bulb, is tolerably soft, but at other places is of almost horny hardness and friability. Histologically, it appears sometimes structureless, sometimes marked very beautifully with parallel striations. The striæ are either immeasurably close or 0·004 (frequently 0·001–·002) of a line apart, and exhibit transitions from the most extreme delicacy to very marked lines.

They have the greatest similarity with those which we see in the wall of the *Echinococcus* vesicles. The structureless mass appears to pass into more slightly or more strongly marked layers which determine the partly longitudinal, partly transverse striation. This often takes on very strange forms when the parts are torn, doubtless in consequence of the folding and tear-

* I retain this term, although the part does not seem to be quite analogous to the organ so named in *H. Argonautæ*.

ing. The substance is little altered by a diluted solution of caustic soda.

The innermost coat of the ductus deferens is generally formed by a layer which strongly refracts light, and when it is stretched looks like a tubular brittle glassy membrane.

Elsewhere when collapsed it has the appearance of a longitudinally fibrous cord, which is easily torn transversely into fragments, and only the local dilatations (for example from 0·02 of a line in diameter to quite smooth clear vesicles of 0·2 of a line in diameter) show its tubular character. One portion is frequently invaginated for a certain distance in a funnel-shaped expanded portion behind it, whereby a swelling is produced. In other places the innermost layer forms the spiral band mentioned by Kölliker. This exhibits considerable elasticity, and its coils are often very close, often far separated, which depends upon the form of the penis. The band has sometimes the appearance of a spirally cut delicate tube, sometimes that of a cylinder, like the snake-toys which are cut out of horn.

Next to this innermost layer the mass of the ductus deferens appears to be longitudinally striated to an irregular extent. Externally again it becomes circularly striated, and not unfrequently some layers appear to be more sharply distinguished from the rest. In the midst some portion will frequently be found wholly structureless, and quite external to the ductus deferens; a strongly marked layer has again all the characters of a so-called vitreous membrane.

In the penis the whole ductus deferens, without reference to its contained spiral band, sometimes forms spiral coils of much greater extent, in which the outer layers of the penis take but little part.

Many modifications of the ductus deferens occur which appear to indicate different stages of development. Instead of the usually tolerably solid enlargement at its commencement (Kölliker, pl. 2. fig. 11 *d*), there exists at times a somewhat large pyriform body which attains a few lines in length, and the larger it is so much the softer are its contents. In its axis, however, one can already distinguish the commencement of the inner denser tube, which further on in the ductus deferens incloses or forms the spiral band.

In one of the specimens without any externally visible penis there projected from the cleft in the back a transparent, pointed, ovate vesicle of a few lines in length, which contained merely a fluid, and at its fixed end was drawn out into a more delicate fine tube of about the same length. The latter appeared when the vesicle, in consequence of being frequently touched, detached itself, and was evidently formed analogous to the ductus deferens; it consisted of a longitudinally striated cord (*i. e.* perhaps a folded tube) and an external, distant, structureless, partially laminated sheath. The larger vesicle therefore may perhaps be considered as an earlier form of development of the bulb, with which the vas deferens generally begins. Other changes in the latter and in the penis appear to belong to a later period. In two *Hectocotyli* which were met with in copulation upon female *Tremoctopoda* (*vide infra*), the abdominal capsule was also open and empty, probably in consequence of long lying in water. The penis, however, with the external part of the ductus deferens plainly visible in it, was distinguished on both occasions by a length of an inch and a half. It passed out of the skin, not in the middle line, but nearer to the right-hand series of suckers, and close to the penultimate pair, which plainly arose from its being torn. Its outermost third appeared to be similar to the whole free part of the penis in other cases; the two upper thirds were thinner, as if pulled out longitudinally. After the skin was taken away from the place of exit of the penis as far as the abdominal capsule, the portion of the penis lying below it was seen to pass below the axis obliquely towards the last sucker of the left side, and there cease. This inner part of the penis formed a fusiform enlargement, which appeared to be hollow. The outermost layers of the penis passed into the surrounding fibrous tissue, but the connexion with the axis was no longer recognizable. In all probability these changes of form of the penis and ductus deferens are connected with the function of copulation, and a third *Hectocotylus*, in which the outermost portion of the penis was plainly torn off, but the inner end had the same relation as in the other two, had probably already performed this act. Its abdominal capsule also was open and empty. The eversion of the ductus deferens for the purpose of ejaculation, indicated by Von Siebold (*l. c.* p. 411), appears to take place,

and indeed in a peculiar manner, which reminds one of the process of eversion of the spermatophora of other Cephalopoda described by Milne-Edwards (*Annales d. Sc. Naturelles*, 1842).

From the preceding facts I will merely draw the conclusion, that the sexual organs in *Hectocotylus Tremoctopodis* are not only more complicated than in *Hectocotylus Argonautæ*, but that different stages in their development occur, although the *Hectocotylus* possesses in general the same form as that with which we are already acquainted. Our knowledge of this *Hectocotylus* is too imperfect to enable us to give a general interpretation of the generative organs. But its structure and the analogy with the *Hectocotylus* of the Argonaut lead to the supposition that the vesicle which contains the seminal coil is not the testis, but a seminal receptacle, although the mode in which the semen makes its way, and the place of its origin are less demonstrable than in the *Hectocotylus* of the Argonaut.

Next to the generative apparatus, the most striking features in *Hectocotylus Tremoctopodis* are the numerous villi on each side of the back, which Kölliker has with great probability called gills *.

In the living *Hectocotylus* the single villi are contractile, apparently in consequence of the fibres which form a meshwork in their interior. Independently of this movement of their substance, a considerable rhythmical contraction may be observed in the efferent (venous) part of the very rich and frequently anastomosing vascular network which lies in each villus, and which passes from the finer to the coarser vessels, as was stated above to be the case in the *Hectocotylus Argonautæ* and in the Cephalopoda in general. In one instance there were twenty-two contractions in ten minutes.

Since these branchial villi might occur in different individuals in different degrees of contraction, the determination of their size in different individuals appeared to be a matter of some interest. For this purpose the largest group of villi in each of several specimens preserved in spirit was selected. When they were very much developed, their length was about 0·6–1·2 of a

* Do these in any way subserve nutrition within the mantle of the female? (see Von Siebold, *l. c.* p. 389).

line. The smallest were not much shorter, and some were longer. The breadth in the middle of the villi was generally 0·15, hardly under 0·12, but as much as 0·22 of a line. These were *Hectocotyli* with a freely projecting penis.

In two others, on the other hand, whose penis was hidden, the length of the villi was but rarely over 0·6–0·7 of a line, and the most were shorter. The breadth was at the base rarely more than 0·12 of a line, and diminished rapidly to 0·06 or 0·04 of a line. The villi namely, had here the form of a rapidly diminishing and pointed cone, whilst in specimens with well-developed gills the diameter of the gills in the outer half surpassed at times that of the base, and the end was more rounded than pointed.

Since it may be assumed that *Hectocotyli* with larger gills have in general progressed further in their development than those with smaller ones, we have here a further evidence that the penis rolled up under the skin of the latter is a younger stage of development than the common form of the free penis.

The *Hectocotylus* of the *Tremoctopus*, then, is very strongly distinguished from the two others by the want of a pigmented dorsal capsule; by the position of the seminal coil in the capsule at the end of the body, and the peculiar structure of the ductus deferens; lastly, by the presence of gills: and, indeed, from the great discrepancies which exist among the *Hectocotylus*-bearing males of Cephalopods among nearly allied species, we should be prepared for thorough differences among themselves.

Upon the other hand, the analogy of the *Hectocotylus* of the *Tremoctopus* with the others in all essential points is so great, that although there is a complete want of all direct observations, we must assume it to have a similar origin, and that one day an entire male *Tremoctopus* belonging to this *Hectocotylus* will be discovered, the exact investigation of which will doubtless be still more interesting than in the Argonaut. However that may be, all three *Hectocotyli* must be kept in mind in attempting to determine the nature of the *Hectocotyli* in general.

Nature of the Hectocotyli.

With regard to this problem, we must consider, first, their relation to the animal which lodges them in their free condition, and, secondly, to that as whose arm they are developed.

The main point as respects the former relation, which Kölliker first demonstrated for the *Hectocotyli*, may be safely assumed to be—that each of the three forms of *Hectocotylus*, considered as one with the animal upon which it is developed *, forms the male factor with respect to a particular kind of female Cephalopod; *Argonauta*, *Tremoctopus* and *Octopus granulosus*, Lamarck, *O. Carena* †, Verany. The evidence of this consists in the following facts :—

1. No other males of the Cephalopoda mentioned are known. All Argonauts ‡ of the ordinary form with velate arms, and all individuals of *Tremoctopus* which have been dissected, were females with ova. To the Argonauts enumerated by Kölliker I can add fifty others of every size, and to the thirteen individuals of *Tremoctopus*, thirty which I have examined with reference to this matter. As has been said, nothing is known respecting the *Octopus*.

2. Most of the free *Hectocotyli* carried semen demonstrably; and it is very probable that the others had done so. To the fifteen *Hectocotyli Tremoctopodis* fourteen others may be added in which this was certain, whilst in four the demonstration failed on account of the emptiness of the capsule. In Cuvier's *Hectocotylus Octopodis* Dujardin found spermatozoa. To the six *Hectocotyli Argonautæ* enumerated by Kölliker, I can add thirteen which all carried the white sac under the pigmented dorsal capsule, and as often as this was opened it was found to contain spermatozoa. To these free *Hectocotyli* are to be added the Argonauts which carried a *Hectocotylus*-arm inclosed in its sac. All the specimens, which were carefully examined, contained semen either in the sac of the *Hectocotylus*-arm or in the testis.

Respecting these animals, indeed, doubts might be raised as to the identity of the species with the common Argonaut, on

* *Hectocotylus Tremoctopodis* questionably.

† If these be different, there will be four species.

‡ Verany (p. 54) cites a solitary statement of Leach that he had found a male Argonaut.

account of the want of both the expanded arms and the shell. But, in the first place, the similarity of the *Hectocotylus*-arm with the free *Hectocotylus* speaks for that identity. Next, the mode in which they occur: during a few days only did I obtain the animals with the *Hectocotylus*-arm and Argonauts of the ordinary kind in any quantity together. The latter were partly larger ones with shells, partly also not more than 2–4 lines long, and these, like the males, had no shell, at least as I obtained them, while the expanded arms were already easily recognizable. The colour and remaining form of the body were, however, in such close agreement with those of the male animals *, that the presence of the expanded arms and afterwards of the shell must be considered not to be specific, but to be sexual differences. It is perhaps not without importance, that these vela with a kind of mesentery on the twisted axis of the arms occur in females of that species whose males carry an arm so excessively developed, which however belongs to a different pair from the vela of the female. The same probably holds good of *Tremoctopus*; for in this, as I shall elsewhere show, the two upper arms have not the shape which is commonly figured, but form, when, as rarely happens, they are well preserved, elongated lobes, which excite as much surprise by their enormous size as by the extraordinary magnificence of their coloration.

It may be expected that the male *Tremoctopus* may have such a structure, as to have been described as some other kind of *Octopus*. Since Cuvier says nothing of any difference in those Octopods which lodged the *Hectocotyli* from the other which carried the *Hectocotylus* as an arm, it seems that the male, as which the latter no less than Verany's specimen of *Octopus Carena* must be regarded, in this case is not strikingly different from the female.

3. The anatomical agreement of the suckers, &c. of each *Hectocotylus* with those of the Cephalopod female upon which it occurs, has been especially made out by Kölliker.

4. In like manner the exclusive association of each *Hectocotylus* with its kind of female only. Up to the present time free *Hectocotyli* have only been found in the society of female Cepha-

* Even the bundles of hairs described by Kölliker (*Entwickelungsgeschichte d. Cephalopoden*) were present as in the females of the size of a hazel-nut. In larger specimens I no longer found them.

lopoda, and indeed, as Kölliker observes, only upon females with ripe ova. I have myself found the free *Hectocotylus Argonautæ* only upon the inner surface of the shell, or upon the ova, or fixed or creeping upon the animal itself, and I can affirm that among the many Argonauts, less than a nut in size, which I have examined, I never found a *Hectocotylus*. The *Hectocotyli* of the *Tremoctopus* were almost all fixed in the mantle-cavity; a few crept about in its vicinity externally, or lay at the bottom of the vessel in which the *Tremoctopus* was contained; since, as Kölliker has stated, they usually leave the dead animal.

5. Direct testimony that the *Hectocotyli* play the part of males to their female Cephalopoda is afforded by two observations of a perfect copulation in *Tremoctopus*.

Upon the 2nd of August two large specimens of *Tremoctopus* were brought to me at the same time, each of which carried in its mantle-cavity a *Hectocotylus*, fixed as usual in the neighbourhood of the gills. Upon pouring water on them, it was seen that the penis of each was inserted far into the opening of the right oviduct. Both of the *Hectocotyli* moved vivaciously, and appeared to be very angry that their endeavours were disturbed. Since it was late in the evening I was obliged to defer further examination until the following morning, when I found both *in situ*, but dead. Both *Hectocotyli* were distinguished by the length of the penis; on endeavouring to draw it out of the oviduct it was held pretty fast, and if let go was retracted again for a certain distance; one might so allow half an inch of the penis to glide in and out. This resulted from a very elastic filament, which, from the point of the penis, projected in deeper; it could be drawn out for an inch from the opening of the oviduct with the penis, and then when it finally gave way it slipped back again. In both cases this thread did not exactly enter at the point of the penis, but somewhat behind; and then in its further course it could be clearly identified as the inner part of the formerly-described ductus deferens.

The right oviduct of the *Tremoctopus* possessed, besides the chambered gland, two dilatations whose walls were greatly softened. The external enlargement was little larger than upon the left side, and contained, together with mucus, merely a portion of the thread torn off from the penis, which has been mentioned. The second larger expansion contained the very singularly con-

structed continuation of this; I will only remark that there hung therein a solid white reniform body of some lines in diameter which consisted wholly of spermatozoa. These were quite similar to those which are usually found in *Hectocotylus Tremoctopodis*, and it is therefore unquestionable that these *Hectocotyli* also serve to fecundate the female *Tremoctopoda*.

The observation of peculiarly-formed masses of spermatozoa far back in the compartments of the oviducal gland itself, was repeated in many specimens of *Tremoctopus*, and it seems almost as though this gland had at least in part the function of a spermatheca; though indeed its relations in other Octopods do not well agree with this view. On the other side of the gland I found no semen, neither in the two copulating *Tremoctopoda* nor in others; but I will so much the less question the possibility of its penetration as far as the ovarian capsule, as the portion of the oviduct between the gland and the ovary is remarkable for its conspicuous ciliary epithelium. A similar epithelium invests also the folds of the ovarian capsule itself which converge towards the internal aperture of the oviduct; it is found there over a considerable space, and finally extends through the so-called water-canal described by Delle Chiaje and Krohn in *Tremoctopus* and *Eledone*, which reaches from the posterior side of the ovarian capsule towards the lateral compartment.

For *Argonauta* I can bring forward no such complete observation, yet the copulation and fecundation by the penetration of the appendage of *Hectocotylus Argonautæ* into the female sexual aperture become very probable from the following facts.

The ovarian capsule of an adult Argonaut contained a filiform body, which, from its form, from the lobe at the thicker end, and from its minuter structure, was certainly the torn-off appendage of a *Hectocotylus Argonautæ*. Attached to it were very diffuse masses of spermatozoa in lively motion. In another very large Argonaut I had sought in vain for *Hectocotyli*. After cutting up the intestines, and especially the generative organs in many directions, I found in the water used for washing the parts, three filaments, which were the appendages of so many *Hectocotyli*.

Functionally, then, the appendage of *Hectocotylus Argonautæ* is to be compared to the penis of *H. Tremoctopodis*, although perhaps the appendage is not always intended to reach the ova-

rian capsule, and may have been a result of some accident to the *Hectocotylus*.

The state of polygamy in which many females of these Cephalopods live is worthy of remark. Cuvier (Laurillard) found three *Hectocotyli* in the mantle of an *Octopus*; Kölliker, among twelve *Hectocotyli* of the *Tremoctopus*, once found three together, and twice, two; Von Siebold found among three, two together; I among eighteen found four together once, and three times, two upon one specimen. I also met with two *Hectocotyli* upon one Argonaut, twice.

Since it is improbable that the *Hectocotyli* can pass from one female to another, either the number of the males must be greater than that of the females, or many of the latter must altogether despair of the society of the former. On the other hand, it seems that the many *Hectocotyli* for one female are *οὐκ ἀποφώλιοι*, as Homer says of the *εὐναὶ ἀθανάτων*. In the oviduct of one *Tremoctopus* were found two distinct, but for the rest almost identical seminal masses, each with its appended tubular filament, and many such fragments appeared to indicate something more than bigamy.

This is perhaps connected with the manner in which at least a portion of the Cephalopoda here referred to lay their eggs. The ova of *Tremoctopus* and *Argonauta* are, it is well known, found in groups, each of which is attached to a delicate stalk. These stalks are in the Argonaut fastened to the convoluted portion of the shell; in *Tremoctopus* to a principal stem some lines thick. The ova of each such single group are as a rule at about the same stage of development; whilst the different groups vary so greatly, that in the larger bunches we frequently meet fresh-laid ova in company with perfect embryos. In this case a regular progression may frequently be detected, so that development gradually advances from one end to the other of the whole bunch. In one bunch of ova of *Tremoctopus* there was furthermore this distinction between the two ends of the principal stem: that the end which carried the most fully-developed embryos had a brownish, wrinkled, old appearance; while that in which the ova were undeveloped was clearer, smoother, softer, and fresh-looking. Between the two were transition-states. The size of each group which has a distinct thinner stalk answers

pretty closely to the quantity of ova which we often find in *Tremoctopus* in a dilatation of the oviduct, which, on the outer side, immediately follows the gland. The ova which we find in the part of the oviduct before the gland, as well as in *Argonauta* in the beginning of the oviduct, are as yet only provided with their separate proper stalks, which are delicate, but already somewhat long; these become united in the outer part of the oviduct into a group with a common stalk, and thence they probably remain here for a considerable period. It may therefore well be, that the different groups of a large bunch of eggs are attached at different times, and although the duration of the intervals is wholly unknown, it may be imagined to be not very small, and perhaps too considerable to allow of the fecundation of all the ova by a single previous copulation. Such ova belonging to different periods might be fecundated by many *Hectocotyli* at different times.

Inasmuch as it has been said that the Argonaut is hermaphrodite, I beg expressly to observe that nothing which I have ever noticed favours this conclusion. In the male specimens the testis lay where otherwise the ovary would be found, and of the latter there was no trace; whilst in a female of 3 lines long it was already very perceptible, and characterized microscopically by ova of 0·02 of a line in diameter. Besides, the want of the velum upon the arms of the *Hectocotylus*-bearers shows that these are quite separate individuals from the females.

If now with regard to two kinds of *Hectocotylus* the anatomical fact is established, that they are developed as arms of perfect Cephalopods, and also that all three *Hectocotyli* very frequently occur isolated, there is a question which promises to be one of a more general interest, viz. What is the relation of the free *Hectocotylus* to the animal from which it has detached itself?

1. That the *Hectocotylus* stands still less in the relation of a parasite (Cuvier) to the animal as whose arm it is developed, than to that in whose mantle it resides, is clear. I will only call to mind, how from the very first all observers have brought forward the striking similarity to a Cephalopod-arm; they have not, however, come to the readiest conclusion, that it *is* such an arm, without many deviations.

2. That Madame Power also wrongly imagined the *Hectoco-*

tylus Argonautæ to be a vermiform embryo of the common *Argonauta* (*vide supra*) has been already shown by Kölliker.

3. Kölliker brought forward formerly the view that the *Hectocotyli* as male individuals are the independent equivalents of the female Cephalopods. According to the present state of knowledge, this view can be tenable only under two suppositions. Either, one must assume an alternation of generations in its wider sense between the *Hectocotylus* and its previous supporter; or, after the separation of the *Hectocotylus* from the rest of the body, it must be regarded as the representative of the individuality, having thrown off the remainder as so much no longer useful ballast.

Against the former view of a kind of alternation of generations however, too many objections at once arise; among others, the development in the place of one of the eight typical arms; the imperfect organization as regards the other generations; further, that the alternation would take place merely in the males; whilst the females of *Argonauta* and *Tremoctopus* are known to lay eggs from which individuals similar to them proceed. Lastly, the presence in *Argonauta* of a testis with perfect semen, which probably passes thence into the *Hectocotylus*, opposes altogether the hypothesis that the latter is a male generation proceeding from an asexual gemmiparous one.

For the other supposition, that the *Hectocotylus*, together with its producer, forms only one animal, but after its separation must be regarded as a continuation of the whole, because it is the means of propagation of the species, analogous cases might be adduced of certain animals in which the organs of individual life retrograde in relation to those of the propagation of the species.

It might be instanced that many Echinoderms, for example, are produced by budding from larvæ, which then waste away; and herewith might be compared the surprisingly great and rapid development of the *Hectocotylus*-arm, as contrasted with the small size of the other arms*. But before drawing such comparisons, further observations must be obtained upon the duration and mode of life of the two separated moieties of the

* In my specimens not more than six pairs of suckers are distinctly developed upon three arms.

original animal. For we know as little how long the isolated *Hectocotylus*, as how long the seven-armed Cephalopod, lives; whether the latter produces new *Hectocotyli**, or passes through yet other metamorphoses. In this respect it is remarkable that male individuals of only a very small size relatively to the females have been observed, and that, independently of sex, they exactly resemble the very young females. The circumstance also that many of the small animals had a tolerably advanced mass of semen in the testis, and that others already carried perfect semen in the seminal sac of the *Hectocotylus*-arm, rather indicates that these males do not grow large, for the ova of females of the same size are nowise developed to the same extent. If large male Argonauts occur, they have been without doubt overlooked in consequence of their wanting the expanded arms and the shell. The specimens of the *Octopus* described by Verany are indeed considerably larger; and Cuvier says nothing about the size of the animals which bore the *Hectocotyli* either in the mantle or as an arm. Yet the case of an *Octopus*, brought forward by Verany, which, in the usual place, had merely the pedicle without an arm or vesicle, is the only direct evidence for the continued existence of the Cephalopod which has cast off the *Hectocotylus*.

Until more light is thrown upon these relations, it seems unnatural to assume that all the most important organs of an animal, the central organs of the circulating and nervous systems, the apparatus of sense and digestion, and so forth, are thrown off *en bloc*, and that the remainder with the semen, which is not even produced in it, should continue to represent the individual.

4. If for the present then the *Hectocotylus* can hardly be considered to be an entire individual, it only remains to regard it as a separated portion of the whole.

Costa has expressed the view that the *Hectocotylus Argonautæ* is the spermatophore of the Argonaut (*Annales des Sciences Naturelles*, 1841, p. 184). The *Hectocotylus* might be rightly so

* In favour of a regeneration of the cast-off *Hectocotylus*-arm we have the fact, that not uncommonly this occurs with other arms. A small conical process covered with a number of small suckers sprouts forth from the torn place of the arm.

called, if the word is to be taken in its general sense; but it can certainly not be classed together with the well-known seminal cases of other Cephalopods which at present bear that name. These spermatophora are mere capsules composed of a no further organized mass, whose movements take place from purely mechanical causes. They are seminal machines, which might as well be called a secretion, if the semen is to be so denominated. The *Hectocotyli*, on the other hand, are composed of different organs and of almost all the elementary tissues which exist, in the same condition as they are found elsewhere in the living body. I will not neglect, however, to draw attention to the analogy which exists in many respects between the spermatophora and the structure above referred to in *Hectocotylus Tremoctopodis*, as the ductus deferens. In both the seminal mass is fixed to a spiral band contained in a sheath, and its uncoiling appears to be connected in the one case as in the other with the extrusion of the semen. The substance of the spermatophora, as of the ductus deferens, is a mass which exhibits transitions from a less to a more considerable consistence, and also from a complete absence of structure to a striation, which, however, is not produced by any peculiar elementary parts. The substance of which the capsules and pedicles of the ova are formed is similar, and in the oviduct of *Tremoctopus* we find masses, of which it is not easy to say how much proceeds from the *Hectocotylus* and how much from the female herself. Should this analogy, upon which I will not enter further here, be confirmed, the *Hectocotylus Tremoctopodis* might at most be called a spermatophore-bearer.

In any case, the *Hectocotylus* of the Argonaut (and probably also the two others) stands in the relation to the rest of the animal, of an arm, which is at the same time penis and ductus deferens. When separated it may be compared with any other part, which separated from a living individual, yet preserves for a certain time a given amount of vital properties. How far, as regards amount and duration, this may extend, cannot be determined *à priori*, and the *Hectocotyli* may perhaps surpass all hitherto known instances.

Nothing can better illustrate the character of their movements, than that Laurillard, Delle Chiaje and Kölliker were led thereby

to hold them for decidedly independent animals, and every future observer will be unable to avoid the same impression*.

The circulation of the blood of the *Hectocotylus*, although its course is only imperfectly known, is very lively and rhythmical. It should be observed, that in detached arms of *Tremoctopus* a rhythmical movement of the veins from the periphery to the centre continued for half an hour after separation from the body, although the animal had been dead for an unknown time. The protracted contractility of separated portions of the Cephalopoda, for example of the skin with the chromatophora, is also already known. Yet in the whole male Argonaut the *Hectocotylus*-arm was the part in which the reflex movement ceased latest, since it continued to make apparently voluntary movements for many hours after these had ceased in the rest of the animal. How long the movement, and indeed the existence of the *Hectocotyli* endure after their natural separation is altogether unknown†, but probably for a considerable time, if copulation be not effected; if indeed they do not exist afterwards.

The presence of the appendages described as gills in *Hectocotylus Tremoctopodis* is very remarkable: since they do not occur in other Cephalopod-arms and *Hectocotyli*, and since, like the penis, they appear to become still larger in detached *Hectocotyli*, it is to be concluded that the *Hectocotylus* in question is originally intended to have a longer separate existence. But the other *Hectocotyli* also are evidently by no means torn off accidentally, but from the manner of their occurrence as well as

* Verany mentions in comparison the gill-processes of Eolidæ, which, when detached, continue to move for many hours.

† Since it is not easy to keep Cephalopoda with *Hectocotyli* in confinement long enough, it will be desirable to pay particular attention in future to their occurrence at particular seasons of the year. Verany obtained the *Octopus Carena* at different seasons; Kölliker obtained the *Hectocotylus Tremoctopodis* in August and September pretty frequently; that of the Argonaut again but rarely. I found most Argonauts without *Hectocotyli* before the end of September, but at that time and in the beginning of October the majority of the large specimens possessed them. In the end of July and the beginning of August I obtained *Tremoctopoda* pretty frequently, and usually with *Hectocotyli*; on one occasion there were eight of the latter in one day. Subsequently the *Tremoctopoda* occurred only singly, and no longer contained any *Hectocotyli*. Hence the deficiencies in my account of the *H. Tremoctopodis*, since I erroneously expected always to obtain the same supply as at first.

the structure of their place of attachment, they are intended to be detached*. In all probability, finally, the thin appendage of the *Hectocotylus* in *Argonauta* and *Tremoctopus* finds its way into the female sexual aperture only after the separation, for we find almost all *Hectocotyli* filled with semen, and the penis of *Hectocotylus Tremoctopodis* often is in an apparently virgin condition. This is easily possible, considering the lively twisting movements which the appendage in both *Hectocotyli* makes, even independently of the rest of the body, and in *Hectocotylus Tremoctopodis* it is rendered still more easy by the circumstance that in the other portions of the penis the epithelium forms a multitude of recurved hooks, the hinder edge of each cell riding on its neighbour. It is to be considered, however, whether preliminary acts of coition do not first determine the separation of the *Hectocotylus* from the rest of the animal.

It is remarkable enough, anatomically, that certain Cephalopod males should be distinguished from those of the immediately allied species by the presence of the *Hectocotylus*-arm; but the facts adverted to render the relations of the detached *Hectocotylus* so peculiar, that one is forced either to remain in doubt, or to come to the conclusion that the line of demarcation between independent animated beings, and such as are not so, is by no means so distinct as the schools draw it.

It is, however, hardly the time at present to draw any theoretical conclusions, when so many matters of fact remain to be inquired into with regard to the known species of *Hectocotylus* (and there may be others), by which perhaps all that has been done may be upset again; for what has been stated here can only indicate in what direction future investigations must be undertaken. I thus sum up the chief results:—

1. Perfect male Argonauts occur distinguished from the females, which only have hitherto been known, by the absence of the expanded "vela" upon the two upper arms.

2. These male Argonauts carry the *Hectocotylus Argonautæ*

* It is important to know whether changes in the size and form of all *Hectocotyli* occur after their separation; whether, for example, the coalescence of the everted edges of the skin in *Hectocotylus Argonautæ* happens before or after separation from the rest of the animal. In my free specimens the pigmented capsule was in all cases fully formed.

(D. Ch.) in a pedunculated sac in the place of the third arm of the left side.

3. The thick end of the *Hectocotylus* is fixed to the pedicle, while the thin coiled-up part is free.

4. By the bursting of the sac and the eversion of its edges, the pigmented capsule on the back of the *Hectocotylus* arises.

5. The testis lies in the abdomen of the whole animal, the external aperture of the ductus deferens being near the point of the *Hectocotylus*-arm, whose thin appendage has at the same time the function of a penis.

6. In the axis of the *Hectocotylus* there lies a chain of ganglia.

7. It is not to be supposed that the *Hectocotyli* are developed as vermiform embryos in especial bunches of ova.

8. The *Hectocotylus Octopodis* of Cuvier, which Verany has shown to be the arm of an *Octopus*, is mainly distinguished from the *Hectocotylus Argonautæ* by its size, by the presence of a capsule at the free end, and by its development as the third arm on the *right* side of the *Octopus*.

9. The *Hectocotylus Tremoctopodis* of Kölliker is distinguished by its gills, by a peculiar structure of the ductus deferens, and by the want of a pigmented dorsal capsule; but it possesses a ganglionic chain in its axis, its penis is a more delicate prolongation of this, like the appendage of the *Hectocotylus Argonautæ*, and its cleft abdominal capsule is to be compared to the lobe upon the appendage of the latter.

10. The *Hectocotylus Tremoctopodis* is thence to be considered analogous to the two other *Hectocotyli*, although the animal as whose arm it is developed is not at present known.

11. Each Cephalopod with a *Hectocotylus*-arm is to be regarded as the male of the corresponding female Cephalopod.

12. The *Hectocotyli* are intended to separate from the rest of the body, and are then received and lodged by the female.

13. In this condition they have apparently independent motion and circulation; they contain perfect semen; and in *Tremoctopus*, as also probably in *Argonauta*, a copulation with the female animals takes place.

14. The *Hectocotyli* are not comparable to the spermatophora

of other Cephalopoda; but perhaps the so-called ductus deferens in *Hectocotylus Tremoctopodis* is similar to these.

15. The free *Hectocotyli* can by no means be regarded as independent animals.

Note by Professor Kölliker.

I desire to take this opportunity of stating, that I have convinced myself of the truth of the most important of the discoveries made by M. Müller, by examining the Cephalopods which he has brought, and that I entirely agree with his view of the relation of the *Hectocotylus Argonautæ* to the male Argonaut. As it now appears, I was led formerly to put too great a value upon the statements of Maravigno and Madame Power, and I was thence induced to consider the *Hectocotyli* as male Cephalopoda which were developed as such in the ovum. It appears now that I was indeed right in the main, when I claimed the *Hectocotyli* as belonging to the Cephalopoda; but that they are not complete animals, but only parts of them, separated indeed in a very strange manner, and by the great independence of their organization and vital manifestations forcibly resembling independent animals.

Kölliker.

EXPLANATION OF FIGURES 1 AND 2 OF PLATE I.

(Both figures are magnified somewhat more than four times.)

* Represents the natural size.

Fig. 1. The perfect male Argonaut seen from the left side: the numbers indicate the pairs of arms; the second and fourth arms of the left side are thrown back, in order to show in what manner the sac containing the *Hectocotylus* is fixed by its pedicle in the place of the third arm. Over the exterior of the sac a ridge extends longitudinally.

Fig. 2. A male Argonaut in the same position, only the *Hectocotylus* has come out of its sac. The sucker-bearing portion is twisted once completely round upon its own axis, so that it is seen at first from one side, then from above, then from the other side, then in the ascending portion directly from below, and again upon the same side as at first. The fixed end of the *Hectocotylus* is still covered by the pigmented membrane of the sac; further on the latter is torn longitudinally upon the

sucker-side towards the mouth, and so inverted in consequence of the *Hectocotylus* being bent back, that one looks upon what was previously the inner surface of the sac: the chromatophora glimmer through only indistinctly. The margins of the cleft lie in the concavity of the first flexure; one margin passes before, the other behind the thick end of the *Hectocotylus*; both unite at * on the dorsal side. Between the edges and the white streak which indicate the seminal sac there is a pit, whose inner surface is formed by what was previously the outer surface of the sac. Where the sucker-bearing part of the *Hectocotylus* passes into the filiform appendage (penis), the lobe appears on the back, and from this on each side a fold passes on to the appendage.

[T H. H.]

Article III.

A few Remarks upon Hectocotylus. By C. Th. von Siebold, Professor at the University of Breslau.

[From Siebold and Kölliker's *Zeitschrift* for June 1852.]

I HAVE read with the greatest interest the recent discoveries of Verany and H. Müller as to the true nature of the *Hectocotyli*. I have now, with Kölliker, arrived at the persuasion that Madame Power, through the too great positiveness with which she described the development of the Argonauta in the egg, has partly been the cause of the hitherto erroneous views that have been entertained upon the subject. Since Maravigno, in fact, only reported upon the communications concerning Argonauta made by Madame Power to the Academy of Catania, it is difficult to say for how much share in the error he is responsible by additional careless observations of his own. From the first I was desirous to have a sight of the figures which Madame Power added to her treatise, and which neither Oken, Creplin, Erichson, nor Kölliker had as yet seen. I availed myself of my last visit to Vienna to examine Madame Power's treatise in the *Atti dell' Accademia Gioënia di Scienze Naturali di Catania* (tom. xii.), contained in the Imperial Library, and especially to convince myself of the resemblance of the figures of Argonauta embryos given by Power, with *Hectocotylus*. I found that the complaints made by Oken (*Isis*, 1845. p. 617) about the careless editing of these academical papers were fully justifiable, since even in this Viennese copy of the twelfth volume the illustrative plate of Madame Power's essay was wanting. In accidentally turning over the leaves of some of the succeeding volumes, however, I came in the fourteenth volume upon the missing plate. Figs. 1–4 represent, somewhat magnified, but very coarsely executed, a something which has a remote resemblance to a *Hectocotylus*; one distinguishes an elongated clavate body, one end of which runs out into an acute point, and whose thicker end is provided laterally with a double series of indistinct pro-

minences. Figs. 1–3 exhibit five or six such elevations upon each side. Fig. 4, on the other hand, has ten upon each side. Fig. 4 then differs from the three preceding figures only by the increased number of the lateral elevations, and yet Madame Power says (see Wiegmann's *Archiv*, 1845, vol. i. p. 378, or Oken's *Isis*, 1845, p. 610) of this fourth form, which she supposes to be an embryo three days old, that from this stage elevations like buds gradually arise, provided with a double series of dark points, and that these are the commencement of the arms and their suckers; where, however, in fig. 4 these commencements of the arms are supposed to be, I can by no means comprehend; for this body, described and figured as an embryo three days old, reminds one only of the arm of a Cephalopod with its double row of suckers. Had Kölliker chanced to see these figures, he would certainly have still more strongly believed that the *Hectocotylus* actually leaves the egg in its proper form.

Now that Verany and H. Müller have drawn attention to the external sexual differences of the Cephalopoda, the different accounts given by Aristotle of the sexual distinctions and functions of the *Octopus* acquire an especial value, since Aristotle appears to have been acquainted with the natural history and internal structure of the Cephalopoda to an extent that we must even now consider astonishing. From the following passages, which I here extract *verbatim* from Schneider's translation (*Aristotelis de Animalibus Historiæ*, book x.), Verany and H. Müller, who have produced a new phase in the history of *Hectocotylus*, will learn with astonishment, that Aristotle may fairly contest with them the priority of their discovery of the relation of the male *Octopus* to the *Hectocotylus*-arm. In fact, in book iv. chap. 1, 6 (*loc. cit.*), it is thus written:—"Polypus (such is Aristotle's invariable designation for *Octopus*) brachia sua ad officium cum manuum tum pedum accordat: namque duobus, quæ supra os habet, admovet ori cibum. Postremo autem omnium, est hoc inter cetera acutissimum et solum aliqua parte candidum in dorso (vocatur autem dorsum pars brachii lævis a qua prorsum acetabula collocata sunt) et in extremo bifidum hoc igitur ad coïtum utitur."

In the fifth book, chap. v. 1, we find further:—"Aiunt non-

nulli, marem habere non nihil simile genitali in uno ex brachiis, quod duo maxima acetabula continet; id protendi quasi nervosum usque in medium brachium atque totum in narem (*funnel*) fœminæ inseri."

In the same book, chap. x. 1, lastly, Aristotle returns once more to the sexual distinctions of the Cephalopoda in these words:—"Differt a fœmina mas capite (*abdomen*) oblongiore et id quod genitale vocant piscatores habet in brachio candidum."

The task now remains for those observers who have the opportunity of investigating that portion of the Mediterranean which lies between Greece and Asia, to decide what species of *Octopus* Aristotle understood by his "Polypus," and how far his acquaintance with the sexual relations of the male *Octopus* coincides with the history of the *Hectocotylus* as it has been recently made known.

[T. H. H.]

Article IV.

Investigation of the question: Does Cellulose form the basis of all Vegetable Membranes? By Hugo von Mohl.

[From the *Botanische Zeitung*, vol. v. p. 497 *et seq.*]

In a former paper* I laid down the anatomical and chemical reasons which led me to persist in maintaining the doctrine of the growth of the membrane of the elementary organs of plants propounded by myself and attacked by various writers, and induced me to reject the view, defended by the Utrecht professors, Mulder and Harting, that the outermost layers of those membranes are the youngest and the inmost the oldest. Since that paper was written I have carried through a long series of new observations for the further elucidation of the conditions here in question, the results of which, so far as relates to the chemical† characters of vegetable membranes, I believe may be published with advantage, because they may serve to throw light upon some points as yet unknown, and to refute the chemical evidence brought forward by Harting and Mulder in favour of their view.

In the Essay already referred to, I closely discussed the opposition presented by the deductions drawn by Mulder and Harting on one side, and by myself on the other, from the known reaction of cell-membranes when acted on by sulphuric acid and iodine. My opponents are of opinion that the circumstance of thin recently formed membrane being coloured blue by iodine and sulphuric acid, while in many full-grown cells only the inner layer manifests this reaction, while the outer are tinged yellow by these two substances, gives ground for the deduction that these outer layers have been formed subsequently to the others, and that the inmost layers of the full-grown cells are the same membranes which constituted alone the wall of the young cell. On the other hand, I asserted that this conclusion is too hasty,

* *Botanische Zeitung*, vol. iv. p. 337 *et seq.* Translated in the Annals of Natural History, vol. xviii. p. 145 *et seq.*

† I shall speak of the anatomical conditions on another occasion.

since a particular layer of an elementary organ may undergo a chemical metamorphosis in the course of time, without experiencing on that account any alteration in dimensions, or affording cause for it to be regarded as a new layer in an anatomical sense of the word: I stated that in respect to this metamorphosis we have to consider two possibilities, since it might arise either through the cellulose of which the layer was originally composed becoming dissolved and replaced by some other chemical compound, or through the persistent cellulose becoming saturated by another compound, and hence losing the capability of reacting with iodine and sulphuric acid. For various reasons I declared the latter view, which certainly offers the most glaring contradiction to the views of the chemists, to be the more probable, but I could not distinctly prove it, because I was unable at that time to extract the infiltrated matters from such membranes as offered an obstinate resistance to the action of sulphuric acid and iodine, and in which cellulose could not be demonstrated to exist by the application of those reagents; such a process of extraction being necessary to render the cellulose (which I assumed to form the basis of the membranes) accessible to the action of the iodine. Now, as the following pages will show, I have succeeded in this with all the elementary organs of vegetables, and I therefore assert most distinctly that the walls of all the elementary organs of plants are composed of cellulose; that it is quite inadmissible to draw conclusions as to the period of origin of any given layer of their walls from its chemical conditions, and that in regard to this question anatomical evidence alone is valid.

In order to establish this proposition, I am compelled to enter somewhat minutely into the details of my investigation: if I enter into more extended explanations of the methods I followed, than seems to many altogether necessary, this is to be attributed to the circumstance that I only arrived at determinate conclusions after many unsuccessful experiments, and I wish others to be able to confirm the correctness of my views.

Cuticle stands first of all the structures, in which it is impossible to demonstrate a trace of cellulose by iodine and sulphuric acid. It either completely withstands the action of sulphuric acid, or, if it undergoes a certain degree of softening by this acid,

Fig. 1.

Fig. 2.

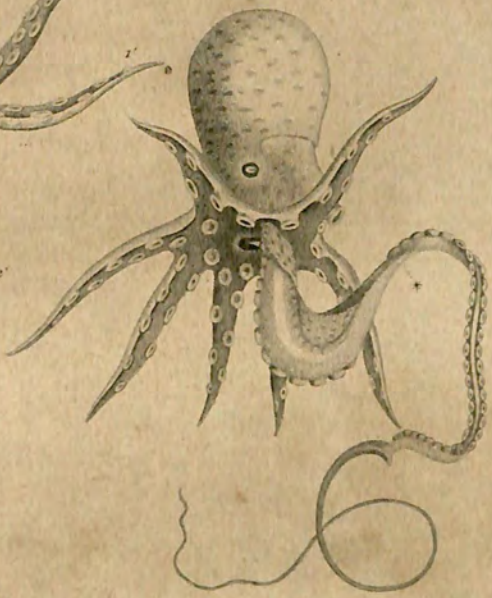

Fig. 3.

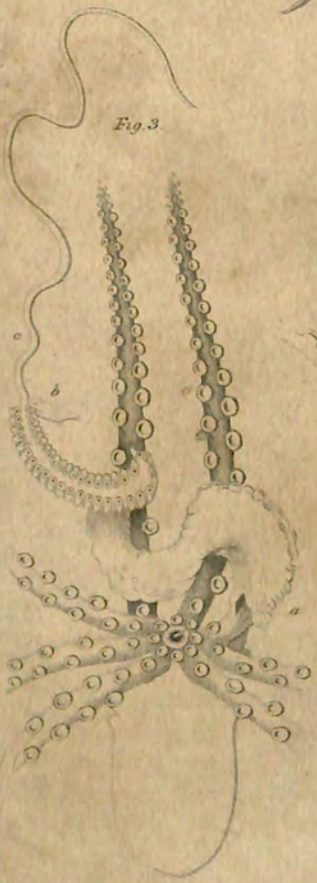

Fig. 4.

this never causes iodine to produce a blue colour in the substance of the membrane, but the latter is always coloured yellow or brown by the application of those reagents. The results are very different when cuticle is subjected for some time to the action of caustic potash. For this purpose a thin section of some epidermis [redacted]essing a thick cuticle, for example that of the leaf of *Aloë* [redacted] must be kept from 24 to 48 hours in a strong solution of caustic potash, between two slips of glass, at ordinary temperatures. The solution I used was so concentrated, that crystals of hydrate of potash were formed when the temperature of the room fell to freezing-point. It is not requisite that the potash should be chemically pure. When the action of the potash on the cuticle was strong enough, the microscope revealed that numerous little drops exuded from it, of a tenacious fluid, not mixing with the solution of potash, but becoming yellow with iodine. The cuticle itself was somewhat swollen up and showed itself (like the membrane of thick-walled cells treated with sulphuric acid) to be composed of numerous superimposed lamellæ, which were not continued uninterruptedly from one cell to another, and hence did not form a connected layer lying upon the epidermis and distinguishable from it, but terminated at the boundaries of contiguous epidermal cells and formed part of their walls. In most cases the epidermal cells had expanded somewhat in the direction of their breadth, and the segments of the cuticle corresponding to the individual epidermal cells had become more or less perfectly separated from each other. When a few drops of a strong tincture of iodine* are applied to the preparation, the latter dried, and then wetted with water, the cuticle acquires as bright a blue colour as the walls of the epidermal cells and the subjacent parenchyma. The purity of the colour is increased, as in most cases in which a cellular membrane is coloured blue by iodine without the application of sulphuric acid, by allowing the preparation to dry up once or twice after being saturated with iodine and wetted with water, and then

* In these, as in all the following researches, I used a tincture of iodine, in preparing which I added an excess of iodine, so that part of this remained undissolved at the bottom of the alcoholic tincture. The attempt to apply a tincture made with sulphuric æther instead of the alcoholic, so as to gain time by the rapid drying, was not accompanied by good results, since this tincture did not wet the preparation so perfectly as that made with alcohol.

wetting it again with water, and if requisite also a second time with tincture of iodine.

A similar result is obtained by cutting off a section of the cuticle parallel to the surface of the leaf, and treating it in the same manner with potash and iodine. The cross-sections of the side-walls of the epidermal cells, composed of cuticular substance, exhibit exactly the same appearance as the other thick-walled cells, composed of a number of superimposed layers; between them runs an external membrane common (?) to the two adjacent cells, which has frequently a yellow or greenish colour at the first wetting with water, but becomes likewise blue after a repetition of the operation. When the cells have separated from each other, this outer membrane is torn irregularly and hangs in fragments attached to one or other of the contiguous cells.

The cuticle of other fleshy or leathery leaves, for instance of *Aloë margaritifera*, *Hoya carnosa*, *Hakea pachyphylla*, *Hakea gibbosa*, &c., behaves exactly in the same way as that of *Aloë obliqua*.

These statements place it beyond doubt that the cuticle of the leaves mentioned is not a homogeneous layer of substance different from cellulose, secreted upon the surface of the epidermis, but that this membrane is composed of separate segments corresponding to the epidermal cells; that it is composed of numerous superincumbent lamellæ of cellulose; and that its chemical diversity from cellulose arises from the infiltration of a substance, coloured yellow by iodine, which not only resists the action of sulphuric acid itself, but protects the cellulose which is saturated with it from the influence of sulphuric acid and iodine. The result is the demolition, in regard to the thick cuticle of thick-walled epidermal cells, of the evidence advanced on chemical grounds against the view I formerly advanced (*Vermischte Schriften*, p. 260) of the structure of cuticle, namely, that it is not a coating over the epidermis composed of substance excreted from the latter, but owes its origin to a metamorphosis of a portion of the outer walls of the epidermal cells.

The infiltrated substance was not totally extracted by maceration of the epidermal cells for 24–48 hours in solution of potash, for the addition of sulphuric acid to the preparation saturated with iodine immediately reproduced the brown colour which is caused in cuticle by these reagents before it is treated with

potash, and the same phænomenon is seen in the wood-cells when the solution of the infiltrated substance is imperfect.

While the above-described action of potash on the cuticular layer of epidermal cells is taking place, a very thin pellicle becomes detached from the outer surface of the epidermis, either in strips, or, when the epidermal cells separate from each other, a piece of this coat remains adherent upon the outer side of each of them. This pellicle is not coloured blue by iodine, but always yellow. When the above treatment is applied to the epidermis of organs in which the outer wall of the epidermal cells is not much thicker than their side walls, and in which iodine and sulphuric acid demonstrate only a very thin cuticle, for instance, of the leaves of *Iris fimbriata*, of stems of *Epiphyllum truncatum*, of the petiole of *Musa*, &c., a thin yellow pellicle remains here also on the outside of epidermal cells coloured blue by iodine. If the epidermis is boiled with solution of potash, this pellicle shrinks together and by longer boiling is completely dissolved, while the epidermal cells only swell up and acquire a beautiful blue colour with iodine. This pellicle, which occurs under all circumstances upon the epidermis, whether it be a portion of its cells transformed into cuticle or not, consists, judging from its different behaviour with potash, of a substance essentially different from the cell-membrane, and is doubtless the same membrane which Ad. Brongniart separated from leaves by maceration, and denominated *cuticle*. It has been confounded, by myself and others, with that portion of the walls of the epidermal cells which is coloured yellow by sulphuric acid and iodine, under the name of cuticle, because the methods of investigation hitherto in use afforded no means of separating these two different parts distinctly from each other. But it is evident that this membrane must be distinguished from the subjacent cells; I therefore propose to restrict the name of cuticle to it alone, and to apply the term cuticular layer to that part of the epidermal cells which becomes coloured yellow by sulphuric acid and iodine. The cuticle exists on all cells exposed to the air, without exception; if any one choose to ascribe it to a secretion of the epidermal cells, I have no objection to offer to the notion; but it would be difficult to bring forward any proof of its correctness; and perhaps we ought to regard the circumstance that this cuticle

is marked with raised lines in many plants, as a proof that it is not to be considered simply as a hardened excreted fluid, since possibly those lines ought to be looked upon as a proof of definite organization.

The researches of Mulder and Harting have made known that sulphuric acid and iodine do not demonstrate the existence of cellulose in *cork* any more than in cuticle; any one may readily convince himself of the correctness of this statement in the cork of the cork oak, of the elder, &c. The cells also of the nascent suberous layer, in their earliest condition, while still covered by the epidermis, exhibit the same yellowish brown colour on the application of the said reagents, as developed cork, even in those plants in which the cork never attains any considerable development, for instance in *Cereus peruvianus*. The conclusion drawn from the absence of a blue colour, that the membrane of cork-cells contains no cellulose, and is composed of a peculiar substance, is, on the other hand, just as groundless as in the preceding case; for a thin section of the cork of the cork oak, which has been boiled in solution of potash until the brown colour it originally assumes has disappeared, acquires as bright a blue with iodine as any other membrane composed of cellulose; in like manner, and also by the application of nitric acid in the way described below, the corks of *Sambucus nigra*, *Acer campestre*, *Ulmus campestris*, and *Euonymus europæus*, show that their cells are composed of cellulose.

It is well known that the layer to which I have applied the name of *periderm*, is, in anatomical respects, to be regarded as a modification of the cork-layer. This circumstance led me to conjecture that this membrane would display chemical characters similar to those of cork. This was confirmed. I subjected the periderms of the oak, of *Cratægus Oxyacantha*, *Betula alba*, and *Plösslea floribunda*, to the action of a boiling solution of potash, after which iodine produced the blue colour. The blue colour was quite clear in the oak and *Cratægus*, but in the other two less pure; the periderm of *Plösslea*, indeed, did not require a very long boiling in solution of potash to produce the blue colour, but only isolated patches of the cells were coloured pure blue, the greater part acquiring a dirty blue tint. The periderm of the birch, which very obstinately resisted the action of the potash,

required a long continuance of the boiling before the iodine would produce the blue colour.

The organs above mentioned, forming the surface of plants, especially the cuticular layer of the epidermis and the cork of the cork oak, and in a less degree the corks of the other plants enumerated, stand, in respect to the chemical properties of the substances combined with their cell-membranes, preventing the reaction of cellulose, in opposition to all those elementary organs which form the internal tissues of plants. In these also the reaction of cellulose is very frequently partially or entirely prevented by compounds combined with them, but caustic potash is not the proper means of reducing the cellulose of these organs into a condition capable of the reaction. Even when, as in many cases, for example in the secondary layers of many wood-cells, such as those of the wood of *Buxus*, potash has this effect, the result is often waited for in vain, and in case of success, the membranes boiled with caustic potash but seldom acquire a pure blue colour with iodine, and a yellow or brown colour is mostly mingled with it. On the other hand, the application of nitric acid is always attended with complete success.

The effect of this acid is perhaps most perfect when the plant to be investigated is allowed to macerate for a long time in dilute acid, at ordinary temperatures; but since in solid woods, when even small fragments are placed in the acid, several months or even a year may easily elapse before the effect of the acid has completely developed itself, this method is scarcely applicable when a large series of observations is to be made with this agent. I therefore substitute a boiling of the substance to be examined in moderately strong acid, for the long-continued maceration; by this means the desired effect is very rapidly obtained, only in many plants the risk is run of dissolving the cell-membrane, or at least some of its layers, by continuing the boiling too long. This inconvenience, however, may be avoided by a little care; for in general the colour of the vegetable structure affords a mark by which we can detect whether the required effect of the acid has commenced and the boiling is to be stopped, or it is to be continued for a longer time. At first, the acid ordinarily produces in the fragment of vegetable substances placed in it, immediately it is heated, a yellow or brown colour, accompanied by considerable effervescence and frequently with the formation

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of vapours of nitrous acid, which colour however soon gives place to a pale yellow, or a complete bleaching of the preparation. When this bleaching takes place, the desired effect is generally attained. I then brought the preparation, if it had not already been boiled between two slips of glass*, on to a glass slider, washed it with water, either dried it perfectly by a moderate heat, or saturated the acid with ammonia, wetted the dried preparation with strong tincture of iodine, let it dry up in the air, and wetted it once more with water for microscopic examination and to produce the blue colour. Sometimes it was necessary to repeat the wetting with tincture of iodine, or to moisten the preparation, saturated with iodine, with water, and let it dry again several times. The whole process is somewhat tedious, but time is saved, by setting to work with a number of preparations at once, and, when they are saturated with tincture of iodine, letting them dry at leisure, by which means we obtain sufficient material for the whole day's work at the microscopic investigation. I have frequently, to save time, assisted the drying of the preparation saturated with iodine by artificial heat; as a rule, however, it is more advantageous to allow the evaporation of the iodine to go on at the ordinary temperature of the room, since even a slight heating may easily cause too strong an evaporation of the iodine.

It is well known that the *parenchymatous cells* of succulent and young organs, in which the membranes are imbued with a comparatively small quantity of the compounds coloured yellow by iodine, require no preparation to render them capable of assuming a blue colour with iodine (see my *Vermischte Schriften*, p. 344). It is different with the parenchymatous cells of older structures which have become saturated with encrusting substances, for instance, the cells of pith and of medullary rays, &c. Very frequently these cannot be coloured blue at all, or only very imperfectly with iodine alone, and do not assume a pure blue tint even with iodine and sulphuric acid, but are tinged with

* In all cases when it is desired to boil a thin cross section of a vegetable structure in nitric acid, it is advisable to place it in a few drops of acid upon a slip of glass, to lay a thickish covering-glass over it, and then place the glass slip (to avoid cracking it) upon a metal plate which can be heated until the acid boils. The most delicate preparations may be boiled in this manner, while they almost inevitably tear up into fragments when it is attempted to boil them in a glass tube or a platinum spoon.

a dirty blue, so that it remains doubtful whether cellulose forms any considerable part of their substance, or even whether it is present at all, at least in some of the layers. These circumstances very readily explain why Mulder, who thought he had an unerring and very delicate test for cellulose in the application of sulphuric acid and iodine, was of opinion that the pith of *Sambucus nigra*, for example, was composed of cellulose only in the earlier conditions, and of a peculiar substance in the full-grown state. But the matter turns out quite differently when this pith is treated in the manner above described with boiling nitric acid, for it then assumes a beautiful indigo-blue colour with iodine.

While iodine and sulphuric acid produce, if not a bright blue, at least a green colour in old parenchyma-cells, and thus the presence of cellulose is placed beyond doubt even by this method of investigation, the brown cells which surround the vascular bundles of Ferns usually resist sulphuric acid as obstinately as even cuticle, and it is absolutely impossible to demonstrate the presence of cellulose by its help. In the essay above referred to, I endeavoured to show on anatomical grounds, that this membrane in the Ferns is produced by the transformation of a cellulose membrane, but was compelled to leave undecided whether or not it still contained cellulose in its fully developed condition. The application of nitric acid affords an easy means of deciding this question, and furnishes the proof that this membrane is only prevented from reacting with iodine by its combination with some infiltrated substance. For instance, if the black membrane surrounding the vascular bundles of the petiole of *Aspidium filix mas*, is boiled in nitric acid until its dark brown colour is changed into bright yellow, iodine imparts a beautiful blue colour to the membrane of these cells, the texture of which is not changed in the slightest degree.

In many cases, in the Ferns, other portions of their cellular tissue are so saturated with foreign compounds that they do not react with iodine and sulphuric acid. Among these, for example, are the outer layers of the dark brown petiole of *Adiantum pedatum*, on the cells of which the said reagents do not act at all at first; only when the acid has been in contact with the cells for twenty-four hours does the blue colour which shows itself at

the circumference of the preparation lead to the recognition of the presence of cellulose in those cells, while the membranes themselves remain yellowish brown. Here again a short boiling in nitric acid suffices to render the membranes capable of taking a very beautiful blue colour.

In particular parts of the cellular tissue of *Polypodium percussum*, the outer coat of the parenchymatous cells acquires a yellow colour with iodine and sulphuric acid, while the inner layers swell up and become blue; in a word, they behave in this respect like the outer coat of wood-cells. In preparations boiled with nitric acid the cells are coloured blue throughout; therefore in these also cellulose is the basis of the outer layer, resisting sulphuric acid.

Such cells, resisting the action of sulphuric acid, are more common than would be supposed from what has generally been stated; for many thick-walled parenchyma-cells, in the same way as many wood-cells, assume only a yellow or at most a greenish tint with the said reagents, as is the case in the parenchyma-cells of many Palm-stems, *e. g.* of *Calamus*, of *Cocos botryophora*, in the thick-walled pitted cells of the pith and rind of *Hoya carnosa*, in the stony cells of the winter pear, &c. All these cells assume a bright blue colour with iodine after they have been boiled with nitric acid; the statement of Mulder, that the thick-walled pith-cells of *Hoya* contain no cellulose, is consequently without foundation.

Since nitric acid is capable of rendering the cellulose accessible to the reaction of iodine in cells which more or less obstinately withstand sulphuric acid, it may readily be imagined that this acid never fails us in common parenchyma-cells, in which sulphuric acid and iodine readily produce a blue, when we desire to impart the blue colour to such cells by means of iodine. This always presents itself in the greatest purity, and without requiring the continuance of the boiling long enough to alter the texture of the cell-membrane in the slightest degree. When it is desired to facilitate the anatomical investigation of cells by the production of this blue colour, for instance to examine minutely their pits, which always appear far more distinct in the blue-coloured cells, this method is far preferable to the application of sulphuric acid, from the very fact that it does not

cause any change in the texture of the cells. The blue colour shows itself uniformly, whether we investigate thin-walled, still succulent cells, such as the rind-cells of woody plants or herbaceous vegetables, the cells of the parenchyma of the leaf and petiole, or the dead cells of the pith or medullary rays of old wood. The walls of epidermal cells saturated with cuticular substance, and the cork and periderm of many plants, only, are inaccessible to the action of nitric acid; in this latter respect, however, the cells of the periderm and cork of other plants form an exception, since cellulose can be demonstrated in them not only by potash but also by nitric acid, for instance in the periderm of *Plösslea*, the cork of *Sambucus nigra*, *Acer campestre*, *Euonymus europæus*, and *Ulmus campestris*. Yet in these cases it is generally necessary to boil the preparation for a long time in the acid, and the effect is mostly imperfect, as these parts do not usually become coloured blue completely after this treatment; there exist, however, some structures belonging to the cork system in which nitric acid is capable of producing a perfect blue colour, while only a greenish tint is obtained by the application of caustic potash, for example the spines belonging to the suberous system of *Bombax* and the corky rind of the rhizome of *Tamus Elephantipes*.

The cell-membranes which assume a blue colour after the boiling with nitric acid usually form a very permanent combination with iodine. While in other cases the iodine which has combined with a thin section of vegetable structure usually evaporates entirely or in great part if the preparation is exposed for a couple of days to the air, and may be extracted in a few seconds with alcohol, preparations boiled with nitric acid and saturated with iodine may often be left lying for weeks in the air without the colour becoming perceptibly paler. In particular cases the iodine combined with the membrane obstinately resisted not only exposure to considerable heat, but the action of almost absolute alcohol heated to the boiling-point. By alkalies, on the contrary, especially by caustic ammonia, the iodine may be very quickly extracted from the membrane. Only the cells of a few of the plants which I investigated, in particular those of the petiole of *Cycas revoluta*, formed exceptions to this rule, that the iodine combined very firmly with the membrane.

In all the cases which I examined, the parenchyma-cells assumed a pure blue colour through the entire thickness of their membrane, and no yellow-coloured outer coat could be detected at the boundary between the cross-sections of the walls of two contiguous cells. In like manner the membrane which closed the pits always exhibited a pure blue, or, in cells which were dried and then assumed a violet colour, a bright violet, and here also no trace of a yellow membrane lying between the cells could be seen, as may be very distinctly observed in the cells of the petiole of *Cycas revoluta*, especially on account of the large size of the pits. When such cells, coloured blue by iodine, for instance those of the pith of the elder, of the medullary rays of *Buxus*, the parenchyma-cells of the stem of *Calamus*, the cells of the petiole of *Cycas*, &c., are placed in dilute sulphuric acid, their membranes swell up strongly and finally dissolve entirely, becoming more or less completely bleached in the process. Under this treatment an extremely delicate yellow pellicle comes to light at the boundaries between the cells, to which pellicles small yellow-coloured granules (or drops of a fluid substance?) are in most cases adherent. We are here reminded of an analogous structure described by Mulder and Harting under the name of the "outer cell-membrane," and the "cuticle of the wood-cells." The question then arises whether this pellicle possessed the yellow colour at the time the cells were coloured blue with iodine, or was at first coloured blue like the inner layers of the cell-walls, the yellow colour having been only produced subsequently by the combined action of sulphuric acid and iodine. I regard it as more probable that the latter was the case; for if that pellicle possessed a yellow colour before the operation of the sulphuric acid, we should have an indication of its presence in the transverse slice of the walls of two contiguous cells, in spite of its very slight thickness, and its yellow colour would cause a greenish discoloration of the thin bright blue membrane which closes the pits. Yet all my efforts to discover even a trace of such a yellow membrane, with the application of the strongest objectives, which gave a perfectly faultless image with a great amount of light, were without the least success. Both this circumstance, and above all the observations on the outer membrane of many parenchyma cells, to be mentioned below, lead me to conclude

that this outermost membrane of the parenchyma-cells also is composed of cellulose and is coloured blue with iodine, but that nitric acid is incapable of extracting the infiltrated matters completely, whence results the insolubility of this membrane in sulphuric acid, and the yellow colour which it acquires from this acid. In this respect this membrane would bear a resemblance to the cuticular layer of the epidermal cells, in which caustic potash, like nitric acid here, is capable of freeing the cellulose from the influence of the infiltrated matters so far that it reacts with iodine, but at the same time does not extract these matters perfectly, and render the membrane saturated with them soluble in sulphuric acid.

Among all the parenchyma-cells which I have investigated, those which form the outer part of the pith of a shoot, several years old, of *Clematis Vitalba*, are perhaps the most interesting in regard to the structure of their walls. These cells have very thick walls, and their membrane is composed of a tolerable number of layers which may be easily distinguished. It is coloured yellow by iodine. Sulphuric acid causes the inner layers to swell up, and at the same time they acquire a green colour: under this operation an outer layer which is on an average $\frac{1}{144}$th of a line in thickness, remains wholly unchanged. This layer therefore displays the character of Mulder's "outer cell-membrane." When strong objectives are employed, a delicate line is seen running through the middle of this layer, indicating the boundaries of the contiguous cells. In a cross-section of these cells boiled with nitric acid, the inner layers are coloured deep blue by iodine, and the outer layer just described assumes, according to the amount of action exerted by the acid, a yellow, green, or blue colour. When such a preparation is wetted with dilute sulphuric acid, the inner layers swell up strongly, they are bleached and by degrees dissolved; the outer layer also swells to some extent, but very slightly, and is bleached, remaining otherwise unaltered. If the preparation is placed in stronger acid, this outer layer is also dissolved, leaving behind an immeasurably thin pellicle (with adherent granules) which lie in the middle of it. It is therefore evident that the outer membrane of these cells, which at the first hasty glance might be taken for the outermost coat, is also composed of cellulose, but that it is in-

filtrated either with a greater quantity of that substance, acquiring a yellow colour with iodine, with which the inner layers are saturated, or with some compound different from this, opposing a greater resistance to sulphuric acid, which is so far extracted or altered by nitric acid, that the reaction with iodine occurs in the cellulose contained in this layer, but enough remains to protect this layer from the action of weak sulphuric acid, while in the outermost, immeasurably thin layer, the resistance to sulphuric acid is so great that the latter is incapable of dissolving it.

In reference to the question whether the above-described outer brown pellicle of the parenchyma-cells contained cellulose, the behaviour of the primary membrane of the cells of the horny albumen of *Sagus tædigera* seemed to me of considerable importance, since here I could convince myself not only of the absence of a yellow colouring of this pellicle, as in the other parenchyma-cells, but positively of its acquiring a blue colour. When the membrane of these cells is treated with a very weak tincture of iodine, it is coloured bright yellow, and the primary membrane deep yellow; in such a preparation very dilute sulphuric acid produces a very bright blue in the secondary layers of the cells, and a darker blue in their primary membrane, and under these circumstances, the comparatively great transparency of the cellulose allows one to become quite certain of the purity of this colour and of the total absence of that yellow colour in the outer primary coat. If stronger sulphuric acid is added, the secondary membranes are bleached and gradually dissolved, while the primary membrane turns yellow and becomes coated with fine granules*. Under these circumstances it cannot be doubted that the primary membrane is imbued with a greater quantity of the substance coloured yellow by iodine, but that this is insufficient to prevent the appearance of the blue colour under the action of iodine and weak sulphuric acid; yet its presence may be the cause why a stronger acid does not dissolve this membrane, for it is always found that a membrane resists the action of sulphuric acid more strongly in proportion as it is more deeply coloured by it and iodine.

* The granules, or minute drops (for there is no means of deciding whether they are solid or fluid), are not separated until the sulphuric acid begins to act.

In reference to the characters of thin membranes, the *liber-cells* generally approach to the parenchyma-cells, since ordinarily they do not possess either the great solidity and brittleness, or the dark colour which distinguishes most wood-cells. This greater resemblance between the liber-cells and parenchyma-cells presents itself also in their behaviour to sulphuric acid and iodine, since the former mostly assume a pure blue colour with these reagents. On the other hand, the liber-cells of the arborescent Monocotyledons, especially of the Palms possessing hard vascular bundles, are allied to the wood-cells of the Dicotyledons; they are devoid not only of the softness and flexibility which distinguish the liber-cells of many Dicotyledons, but in many cases they exhibit also a yellow colour, sometimes passing into the deepest brown. I examined the liber-cells of three species of Palm, *Cocos botryophora*, *Calamus*, and the black-fibred Brazilian palms, the wood of which is used for making walking-sticks. When a cross-section of the liber-bundle of one of these is treated with iodine and sulphuric acid, the secondary layers are dissolved and the outer layer of the cells remains behind undissolved, with a brown colour. This outer layer, which, like the above-described outer layer of the pith-cells of *Clematis*, corresponds, according to the characters given by Mulder, to the "outer wood-membrane" of the wood-cells of the Dicotyledons, and would be supposed to consist of a substance different from cellulose, exhibits considerable thickness in a cross section, and in *Cocos botryophora* (where it is about $\frac{1}{100}$th of a line thick) is distinctly pitted. For these two reasons we cannot regard it as the primary membrane of the cells, since in all cases its not inconsiderable thickness and the presence of pits, which do not perforate the membrane completely, but penetrate only to a certain distance on both sides, lead us to conclude that this layer is composed of several superincumbent lamellæ. When a cross section of a vascular bundle of these plants boiled in nitric acid is treated with iodine, exactly the same phænomena present themselves as I have described in the pith-cells of *Clematis*, namely, all the layers of the liber-cells, especially the outer one withstanding sulphuric acid, are coloured bright blue, which proves that this latter also is composed of cellulose. If dilute sulphuric acid is then added to such a preparation, not

only are the inner layers of the cells dissolved, but also the outer, which before this treatment with nitric acid were insoluble in sulphuric acid, and on the boundary-lines between the adjacent cells, as in the parenchyma-cells, remains a pellicle of the utmost delicacy coated with fine granules. Since in these cells also, when very thin sections are coloured only pale blue by a small quantity of iodine, it is impossible to detect by a yellow colour this pellicle insoluble in sulphuric acid, I consider it probable that this possesses a blue colour so long as it is not exposed to the action of sulphuric acid. The presence of this outer thin membrane, and the fact that it is only yellow under the simultaneous action of sulphuric acid and iodine, and blue with iodine alone, may perhaps be still more clearly proved by macerating a vascular bundle of the black palm-wood in dilute nitric acid (which however may require six to twelve months), or boiling it in this acid until the liber-cells are separable by a slight pressure. In this case isolated pieces of variable size of the outer membrane may often be found among the separate liber-cells, and we can then convince ourselves that they are coloured blue by iodine, and only assume a yellow colour when sulphuric acid is added. These are the observations which principally led me to the opinion that the outer membrane of parenchyma- and prosenchyma-cells contains cellulose, since the impossibility of seeing the yellow colour in this membrane in the cross section appeared not perfectly conclusive, on account of its very slight thickness, though at the same time it must be admitted that this circumstance is also of great importance.

Passing to the *prosenchymatous cells of the wood* of Dicotyledonous plants, it is well known that cellulose may be demonstrated in their internal layer by means of sulphuric acid and iodine, but that these layers do not usually, it is true, assume a pure blue colour with these reagents, mostly acquiring only a green tint, which leads to the conclusion that cellulose does really exist in them, but that its reaction is more or less obscured by the presence of a yellow infiltrated substance. Even when, as in the wood of *Taxus*, the resistance to sulphuric acid is very considerable, the presence of cellulose may be shown by applying a very strong acid, which completely destroys the texture of the cell-wall, and then, by adding tincture of iodine diluted with a

great deal of water, the dissolved cellulose (which according to this experiment is dissolved as such, and not as dextrine) is precipitated with a beautiful blue colour. But although these means suffice to demonstrate the presence of cellulose, the application of sulphuric acid is not adapted for the settlement of the question, whether in such solid woods the cellulose forms always the principal mass of the membranes and is only saturated with a foreign substance, or the latter is predominant and the cellulose only a very subordinate constituent. In this case the application of nitric acid removes every doubt, inasmuch as the secondary membranes of all wood-cells become bright blue through their entire thickness with iodine, when they have previously been macerated for a long time, or boiled until disorganized, in nitric acid. The compound, therefore, which Mulder termed the "intermediate wood-substance," never itself forms the intermediate layers of the wood-cells, but is a material infiltrated into them. Since this result is quite universal, I regard it as superfluous to mention particular examples, and confine myself to touching on a few points which may be doubtful.

One of these refers to the character of the internal membrane which lines the wood-cells in *Taxus* and *Torreya*, and of which the spiral fibres running in these cells form part. This inner coat, as was first shown by Prof. Hartig of Brunswick, resists the action of sulphuric acid very strongly and under its influence is coloured yellow by iodine, whence, relying upon these reagents, as Hartig did, one might be inclined to assume that this membrane was composed of a substance quite different from the intermediate layer, and contained no cellulose. The latter is by no means the case, for the above-described treatment with nitric acid demonstrates, by the blue colour which this membrane and its fibres assume, that these also are composed of cellulose.

The second point to be adverted to here, relates to the pits, of which it might be doubtful, from the descriptions which Hartig, Harting and Mulder have given of the structure of cells and the characteristics of the "outer wood-membrane," whether the membrane which closes the outer ends of the canals of the pits is always composed of cellulose. In regard to this, there can be no doubt in preparations of the Coniferæ which have been treated with nitric acid, since it is found that the pits are closed

by blue, although not brightly coloured, membrane, as I have seen most distinctly in the wood of *Taxus baccata* and *Abies pectinata*. But I must expressly remark, that observation of this, as well as of the membrane which closes the pits of the parenchyma-cells, requires a microscope of the highest quality, furnished with very strong objectives; with objectives not of very short focus, *i. e.* unless at least less than a line, even when the image they give is perfectly free from error, the membrane closing the pits will be sought in vain, since the penetrating power of the microscope will be too small.

The most difficult point in the investigation of the wood-cells is that of their outermost membrane (Mulder's "outer cell-coat," Harting's "*cuticle* of the wood-cells").

In the first place, the remark perhaps may not be superfluous in reference to this membrane, that in many wood-cells we meet with a case similar to that in the above-described pith-cells of *Clematis* and the liber of *Calamus* and *Cocos botryophora*, namely, that when a cross-section of the cell is soaked with iodine, layers of two kinds may be distinguished, a thick inner one, very brightly coloured, and a thinner outer one which acquires a darker yellow colour with iodine and might readily be taken for the primary membrane of the cell, *e. g.* in *Buxus*, in particular cells of the wood of *Erythrina caffra* and of many kinds of *Ficus*. This outer layer withstands the action of sulphuric acid much more strongly than the inner, so that a weaker acid suffices to cause a strong swelling up of the inner layer, bringing out a blue or green colour, while the outer layer is quite unaffected and remains yellowish brown. A stronger acid, however, is capable of producing a green colour in the outer layer, or at least of bleaching and dissolving it when the action is allowed to continue for some time. Treatment of a cross section with boiling nitric acid leaves no doubt of the true nature of the conditions, since in a preparation so treated both layers are coloured bright blue by iodine, and dilute sulphuric acid quickly dissolves even the outer layer, so that any confusion of this with the outer cell-membrane is out of the question.

The latter exhibits the same qualities as I have described above of the outer coat of the parenchyma and liber; it is extremely thin, withstands the action of sulphuric acid, and

is coloured yellow by this and iodine. It is just as difficult with this outer coat of the wood-cells as with the outer layer of the parenchyma-cells, to answer the question whether it is coloured yellow or blue by iodine, but similar reasons render it probable here also that the latter is the case. For if a transverse section of a Dicotyledonous wood which has been boiled in nitric acid is soaked with iodine, a yellow membrane may be detected between the blue-coloured cells; if the action of the acid has been more powerful, this yellow colour is more and more lost and passes through green into a perfectly pure bright blue, so that no trace of any yellow membrane lying between the blue cells can be seen here any more than in the parenchyma-cells. This is the behaviour, for example, of the wood of *Abies pectinata, Larix europæa, Taxus baccata, Torreya taxifolia, Buxus sempervirens, Viburnum Lantana, Viscum album, Betula alba, Fagus sylvatica, Clematis Vitalba, Erythrina caffra.* When dilute sulphuric acid is added, the cell-membranes are dissolved with a slow bleaching, and there remains behind a network of immeasurably thin yellowish-brown pellicles, which correspond to the boundaries of the cells.

In most, perhaps in all woods, the intercellular passages running between the wood-cells are filled up by an intercellular substance, which is coloured yellow by iodine and sulphuric acid, and not attacked by the latter, whence one might easily be led to assume that this substance formed a common mass with that membrane of the cells which likewise acquires a yellow colour under these circumstances. But the incorrectness of such a notion is proved by the examination of the preparations boiled in nitric acid, since in these the intercellular substance retains its yellow colour on the application of iodine, while the outer cell-membrane is coloured blue. Whether the intercellular substance of Dicotyledonous woods is wholly free from cellulose, or contains it in a very strongly combined condition in which it is not acted on by iodine, I cannot yet venture to decide. The application of caustic potash to the investigation of this condition entirely failed me, and the application of nitric acid furnished no decisive result. For if the boiling with nitric acid is stopped before the texture of the cells is attacked, the intercellular substance, as above mentioned, remains yellow on the

application of iodine; while if the transverse section of a wood is boiled longer than is requisite to impart to its cells the capability of acquiring a blue colour with iodine, under which circumstance the cells begin to separate from each other, the intercellular substance is no longer found, being dissolved. I hoped to find it in a transition state between these two extreme cases, and then perhaps, if it contained cellulose, to be able to detect this with iodine; and, if I was not deceived, it indeed happened with a few woods, for example, in *Buxus sempervirens* and *Clematis Vitalba*, it assumed a bright blue colour after the yellow had disappeared. This colour however was very pale, and might possibly have depended on a bluish tinge thrown upon the bleached intercellular substance by the surrounding dark blue-coloured cells, so that I do not venture to declare the observations certain, and must leave this point undecided for the present.

To mention some of the examples in which an intercellular substance with the said properties filled up the intercellular passages between the wood-cells, I may name *Larix europæa*, *Taxus baccata*, *Torreya taxifolia*, *Viburnum Lantana*, *Buxus sempervirens*, *Clematis Vitalba*.

When the intercellular substance is dissolved by means of nitric acid, the cells of the wood begin to part from each other. It is difficult to trace accurately the process which occurs here, since the blue colouring of the cell-membrane by iodine, which would greatly facilitate the investigation, does not occur unless the preparation saturated with iodine is allowed to dry up; but this drying causes a contraction and tearing of the membranes, which places the greatest difficulty in the way of detecting what goes on during the separation of the cells. The notion might readily be formed that the separation of the cells resulted from the solution of their outer membrane, as well as the intercellular substance, by the nitric acid, and that the cement which connected the cells together was thus removed. But if I have rightly understood the operation, it is something quite different from this. The outer membrane is not dissolved, as is easily seen when such preparations, saturated with iodine (whether the cells have been separated from each other by boiling nitric acid or by long maceration at ordinary temperatures), are treated

with sulphuric acid, under which circumstances the outer membrane presents itself unchanged with a yellow colour, after the rest of the cell-membranes have been dissolved. The separation of the cells seemed rather to depend upon the outermost layer of the secondary membranes becoming softened into a gelatinous condition, and detached from the primary membrane. The circumstance that the outer layers of the cells are caused to swell up and dissolve in strong acid sooner than the inner, is not uncommonly met with, especially in treating with sulphuric acid half gelatinous cells saturated with iodine, for example, the half collenchymatous cells of the bark, like those of *Erythrina caffra*. In such cases it is very common for the outer layers of the swollen cells to have a brighter blue colour than the inner, and when by a longer action of the acid these inner layers also become perfectly blue, the outer layers are completely bleached. A similar phænomenon sometimes presents itself most distinctly under a strongish action of nitric acid. This is especially the case with the wood-cells of *Clematis Vitalba*, the outer layers of which, when the boiling in acid is long continued, dissolve into an amorphous jelly, which acquires a blue colour with iodine. Such a perfect solution of the outer layers, however, is by no means necessary to bring about the separation of the cells; even a slight softening of the cell-membrane seems sufficient to separate the secondary layers from the outer membrane, and thereby the cells from each other. In favour of this, we have both the microscopic examination of cross sections which have been boiled in nitric acid till the cells have separated, and in which fragments of delicate torn membranes, but no amorphous jelly, are met with between the cells,—and also the circumstance, that in the wood of *Abies pectinata*, which had been macerated for about a year in dilute nitric acid, and in which the elementary organs fell apart on the slightest pressure, the canals of the pits were closed at the outer ends by a thin membrane, which could not have been the case if the outer membranes of the cells had been dissolved. The extraordinary softness which the cell-membranes had acquired, both in this wood and in the hard vascular bundles of the black-fibred palm above-mentioned, when treated in the same way, was remarkable.

In this separation of the cells, the outer coat never seemed to

split into two lamellæ remaining attached to the two adjacent cells, but the membrane situated between two cells remained undivided, separating from both cells, or remaining attached to one of them, which of course must have been accompanied by a disruption of it in other places. When exactly the right period of the action of the acid in which the wood is macerated, has been hit, comparatively large pieces of the outer coat may be often obtained isolated, by tearing up a piece of such wood with a needle, since the cells may be readily extracted, as from a shell, from the chambers formed by the cavities of the outer coat.

Proceeding to the *Vessels*, the different layers of the walls of the forms containing spiral or annular fibres behave in the reverse way to those of cells. In the latter, namely, when they are greatly lignified, the outer layers are usually saturated most strongly with foreign compounds, and therefore offer the greatest resistance to the action of sulphuric acid, while the inner layers, as the youngest membranes, are frequently coloured a beautiful blue by iodine and sulphuric acid; in the vessels, on the contrary, the secondary structures (the fibres) are those which most strongly resist sulphuric acid, and only acquire a yellow or at most a green colour, while the tube on the inner wall of which the fibres are deposited may acquire a bright blue with these reagents. This difference is seen very beautifully in the vessel-like elementary organs, furnished with flat, band-like spiral fibres, of the wood of many Cactaceæ, especially of the *Mammillariæ*. When these elementary organs are treated with boiling nitric acid, both the fibre and the outer coat are coloured bright blue. In like manner the spiral fibres of the vessels of herbaceous plants, for instance of *Asparagus*, may be coloured bright blue after treatment with nitric acid; in the vessels of many plants, however, especially in the spiral vessels of *Sambucus nigra* and the scalariform vessels of *Tree Ferns*, a rather long-continued boiling in the acid is requisite to destroy the green colour and bring out the pure blue.

The pitted vessels of the Dicotyledons approach the wood-cells nearer than the spiral vessels in their behaviour with iodine, since it is their outer layers which are principally infiltrated with the foreign compounds coloured yellow by iodine. But treatment with boiling nitric acid also produces the blue colour in all the

layers here, and not only in the thickened layers of the walls of the vessels, but in the delicate membrane which closes the pits. This was the behaviour, for example, in the vessels of *Sambucus nigra*, *Viburnum Lantana*, *Asclepias syriaca*, *Buxus sempervirens*, *Clematis Vitalba*, *Betula alba*, *Quercus Robur*, and *Tilia*. The outermost membrane of these vessels behaves in every respect like the outer cell-coat of the prosenchymatous cells of wood, and similar reasons to those which testify that the latter contains cellulose are furnished also by the outer membranes of vessels, so that I may refrain from entering into minute details on this point.

The researches of Mulder and Harting have already made known that the wall of the *Milk-vessels* contains cellulose; and in like manner I only think it necessary to state briefly that the elementary organs of that part of the vascular bundles of Monocotyledons which I have described under the name of *proper vessels* (*vasa propria*) in the Palms, and elsewhere, acquire a beautiful blue colour with iodine after treatment with nitric acid.

Looking back over the researches here described, it appears clear that the walls of all the elementary organs of vegetables may be brought, by the action of caustic potash or of nitric acid, into a condition in which they assume a blue colour with iodine, and that the only exceptions to this among all the solid structures of plants, are the *cuticle*, in the strictest sense of the term, and perhaps the *intercellular substance* of the higher plants.

The action exerted by potash or by nitric acid upon vegetable membranes is not merely transitory, enduring only while the action is kept up (as Mulder assumes of the action of sulphuric acid upon cellulose), but is permanent, inasmuch as the membranes which have been treated in the above-described way retain the capability of taking a blue colour with iodine after the active substance has been completely removed, as when the nitric acid is neutralized by ammonia. The question now arises, whether the cellulose itself suffers a transformation by the application of these means, rendering it capable of taking a blue colour with iodine, in the manner starch does, or, whether these means act merely to extract or decompose more or less perfectly the foreign compounds combined with cell-wall, which acquire a yellow colour with iodine, and deprive cellulose of the

power of reacting with iodine. These questions must be answered by chemists, and not by botanists. Yet I may be permitted to allude to two points. A conversion of the cellulose into starch is out of the question, for the cell-membranes treated in the way described remained afterwards, as before, insoluble in boiling water; if therefore a transformation of the cellulose is assumed, it must be into some compound as yet unknown, the characters of which have still to be minutely investigated. For the present the assumption of such a transformation appears to me unwarranted, in so far that the power of the cell-membranes to acquire a blue colour with iodine is the only reason at present existing which can be urged in favour of this, while I have already shown, on previous occasions, that fresh, perfect, unaltered cell-walls of many plants, particularly of young organs, also acquire a blue colour with iodine, which indicates that cellulose possesses this quality, as well as starch, in and by itself, whenever its reaction is not prevented by other compounds united with it. For the present, and until we obtain further explanations from the chemists, it will be simplest to assume that the potash and nitric acid bring about this reaction by removing such foreign compounds from the encrusted membranes.

Looking from anatomical and physiological points of view, and these alone I have occupied in my researches, I believe that I have shown, from the latter, that the reaction of sulphuric acid and iodine upon cellulose is altogether devoid of the trustworthiness ascribed to it, and that the assumption based upon this supposed trustworthiness,—that particular layers are formed of other compounds besides cellulose, in the course of the development of the elementary organs of plants, and that the chemical reaction of the different layers of a vegetable elementary organ therefore affords a certain test of the relative epoch of its development,—is totally devoid of foundation;—that, consequently, all the objections against my theory of the development of the walls of vegetable cells, built upon this basis, are completely untenable, and that in this question anatomical evidence alone can be admitted as proving anything.

[A. H.]

ARTICLE V.

Memoir upon the Hectocotyli and the Males of certain Cephalopods. By MM. J. B. VERANY and C. VOGT.

[*Annales des Sciences Naturelles*, t. xvii. No. 3, 1852.]

THE manner in which the fecundation of some Cephalopods, especially of the Argonaut and of the Tremoctopods, whose females only have been known up to the present time, occurs, is a zoological question of the highest interest. The very recent researches of MM. Kölliker and Siebold having called the attention of naturalists to this point, we have neglected no opportunity of procuring fresh and living animals, by the study of which we hoped to arrive at a definite solution of the problem. We venture to think that our investigations have been rewarded by complete success, at least for one species.

The memoir which we now lay before the Academy relates principally to the *Tremoctopus Carena* (Verany) and the *Hectocotylus* which is derived from it. We shall give, first, a historical summary of the labours of our predecessors; then the zoological description of the species which occupies us, and which was to a great extent unknown up to the present time; lastly, we shall conclude our work by a detailed study of the reproductive organs.

Historical Introduction.

M. Delle Chiaje, at Naples, described and figured in the year 1825* a little animal found by him parasitic upon an Argonaut, to which he gave the name of *Trichocephalus acetabularis*. This animal, when once detached from the *Octopus*, to which it was adherent, swam and crept at the bottom of the water with uneasy movements. It appeared full of life for many hours. M. Delle Chiaje did not doubt that this parasite was one of the Helminthic worms, and placed it in the genus *Trichocephalus* of

* *Memorie sulla Storia e Notomia degli Animali senza vertebre del regno di Napoli; di Stefano Delle Chiaje.*

Rudolphi, although it was provided with a double series of suckers, wishing, as he says, not to burden science with a new genus. M. Delle Chiaje only describes the exterior of the animal. According to him it has a long, round, filiform, very contractile proboscis, attenuated towards its extremity. The body is provided with a double series of alternating and retractile pedunculated suckers, by which the animal adheres to the skin or to the shell of the Argonaut.

M. Laurillard discovered at Nice, upon the *Octopus granulosus* of Lamarck, five specimens of a parasitic animal, which Cuvier described subsequently as the *Hectocotylus Octopodis**. Among these five individuals three were found in the funnel of a female *Octopus*, one was discovered in the same position in another *Octopus*, and the fifth individual "had attached itself to an arm of the *Octopus*, and had transformed it into a kind of sac, into which it had introduced its head, the remainder of its body being external and free." In recurring to this individual, Cuvier adds, "The *Hectocotylus* has attached itself to one of the arms, which it has even almost destroyed, and which it seems to replace in such a manner, that at first sight it might be taken for the arm itself." With our present knowledge, we must conclude from these remarks that one of the Octopods taken by M. Laurillard was a male, which had just disengaged its hectocotyliform arm from the sac in which it had been developed.

Cuvier describes the external form of the body, the suckers, and the internal organization. None of his *Hectocotyli* had the filiform organ, which we shall call the flabellum (*le fouet*), everted from the sac which contains it. Cuvier found at the rounded extremity of the body an alimentary orifice leading into a sac, closed on all sides, and having a yellowish internal surface. This cavity, which Cuvier calls a stomach, is nothing more than the sac opening by a cleft, whose formation we shall subsequently describe. Besides this stomachal sac, the clavate extremity contains another "with stronger parietes, occupied by the innumerable folds of a thread which has the colour and brilliancy of raw silk. One of the *Hectocotyli* ejected this thread very rapidly at the moment of its capture." Cuvier is disposed to look upon this thread as connected with generation. It is in fact the

* *Annales des Sciences Naturelles*, tome xviii. 1829.

seminal thread contained in a spermatophore. Besides these organs, Cuvier describes the muscular tube forming the axis of the body, and continuous with a filament folded up in the terminal sac,—a filament which we have called the flabellum. According to Cuvier, the point of this flabellum is bent back into the body of the animal, and is directly continuous with the seminal thread. We know not to what circumstance we must attribute this mistake, for in all the specimens we have examined, the flabellum has been found completely free at its extremity.

The note which was published at a later period by M. Costa of Naples, upon the *Hectocotylus Argonautæ**, only added to the controversy the opinion of the author, who looks upon this animal as the spermatophore of the *Octopus*. M. Costa's description is besides altogether incorrect, and the figure is as bad as it can be. The sac of the flabellum is represented like a pennant; the extremity of the true spermatophore as a tentacular cirrhus with two points; the convolutions of the seminal thread appeared to M. Costa to be spots formed by little spiral vessels.

M. Dujardin, in arranging the *Hectocotyli* among the doubtful *Trematoda*, thus gives his opinion upon these parasites †:—"I have seen the anatomical preparations preserved in the Museum, as well as an entire specimen; but I confess I cannot comprehend what the thing can be; I am only clear that it is not a Trematode worm. One might call it an arm torn from some other Cephalopod, so similar is the double series of suckers occupying the ventral surface of the *Hectocotylus* to the larger suckers of the *Octopus*: the internal structure is equally muscular, but there is visible in the dorsal portion a long white sinuous and folded thread, which Cuvier could detect only after the action of spirit, and which therefore should proceed from the coagulation of some liquid (spermatic?) substance....."

"It can only be by the study of these objects in the living state that we can decide upon their true nature, and determine if they be not the portions of some Cephalopod detached in order

* *Note sur le prétendu parasite de l'Argonauta Argo* (*Ann. d. Sc. Nat.* 2e série, t. xvi. 1841).

† Dujardin, *Histoire Naturelle des Helminthes ou Vers Intestinaux* (*Suites à Buffon*, 1848).

to subserve fecundation. I can only state, that the long white thread described by Cuvier, whose length is more than a metre, is merely a bundle of very long and delicate, independent filaments, closely resembling the spermatozoa of the Cephalopoda."

M. Kölliker, who during his stay at Messina in 1842 found upon many female Argonauts the *Hectocotylus* described by M. Delle Chiaje, originated a new epoch in the history of this animal. M. Kölliker discovered in addition a new species of *Hectocotylus* upon the *Tremoctopus violaceus*, and obtained some fifteen specimens of it. In examining their structure he very soon convinced himself, to use his own words, that these supposed worms are nothing more than the males of the Cephalopods we have just mentioned.

After having communicated his ideas upon this subject to the Italian Scientific Congress, sitting at Genoa, M. Kölliker published a note in the 'Annals of Natural History,' vol. xvi. 1845. The Manual of Comparative Anatomy, by M. von Siebold, being in course of publication at the same time, M. Kölliker entrusted three specimens of his treasure-trove to M. von Siebold, accompanying them with a manuscript note containing the results of his observations. Upon his part M. von Siebold examined the *Hectocotyli*, and, while confirming many of the conclusions of M. Kölliker, he differed from him with respect to other points of structure. Notwithstanding these discrepancies, M. von Siebold adopted the views of M. Kölliker, who considered these *Hectocotyli* to be the males of the Octopods upon which they are found. The observations of M. von Siebold are contained in his excellent 'Comparative Anatomy of the Invertebrata*,' which is now also extensively circulated through France in a good translation. Lastly, M. Kölliker published a very elaborate memoir, accompanied with figures, in his Second Report of the Zootomical Institution at Wurzburg, for the year 1849†.

M. Kölliker begins by describing at length the form of the *Hectocotylus* of *Tremoctopus violaceus*, specimens of which he met with upon almost all the females of this Cephalopod, which he found in August and September at Messina. He distin-

* *Lehrbuch der vergleichenden Anatomie der Wirbellosen Thiere; von C. Th. von Siebold.* Berlin, 1848.

† *Bericht von der Königlichen zootomischen Anstalt zü Wurzburg.* Leipzig, 1849.

guishes externally two sets of suckers, branchiæ in the form of villosities, and an oval abdomen from whose aperture the penis makes its exit. The skin is composed of two layers; of an epidermis with polygonal cells, and of a corium composed of interwoven undulated fibrils, in the midst of which contractile pigment-cells are deposited—chromatophora such as are met with in all Cephalopods, without exception. The muscular system is composed of bundles belonging to the suckers, and besides of a very strong muscular tube, which serves as a support to the whole body, and in the interior of which is found a cylindrical cavity almost entirely filled by a longitudinal tube which M. Kölliker calls the intestine. The muscular tube itself is composed of three layers of fibres, the median being longitudinal, whilst the other two are circular. M. Kölliker is unable to give any complete account of the nervous system; but having seen under the microscope a true ganglion containing six ganglionic corpuscles, he is certain that nerves exist, and he believes that a fine white thread, which he once met with upon the upper surface of the intestine, is truly a nervous cord. M. von Siebold, on the other hand, remarks, that he has found in the axis of the body of the *Hectocotylus* of the *Tremoctopus* a nervous cord whose greatly developed ganglia correspond in number with the lateral suckers. M. von Siebold does not believe that the *Hectocotyli* have any digestive system. M. Kölliker speaks doubtingly: he describes a longitudinal tube situated in the centre of the muscular tube, which it almost wholly fills. This tube is composed of two membranous layers; according to his account it is closed posteriorly, and terminates perhaps by a fine aperture visible only in the recent animal and situated at its anterior extremity. The tube contains nothing but conical masses, arranged regularly, and exactly corresponding in number to the suckers. M. Kölliker adverts also, as a supplement to this description of the intestinal system, to the existence of small elliptical apertures arranged in line to the number of four or five, upon the ventral surface, below these conical bodies contained in the intestine. These little apertures are prolonged into as many fine canals which are directed upwards towards the central muscular tube; but he could not decide exactly if they entered

into the muscular tube to communicate with the conical bodies, or if they were merely cutaneous glands.

We can easily satisfy the doubts of M. Kölliker upon this matter. His so-called intestine is only a central blood-vessel; the conoid masses seen by him in this "intestine" are the ganglia of the nervous cord situated below the vessel and not within it; whilst the canals with their fine apertures are only the nerves passing from these ganglia and terminating in the skin. The branchiæ described by M. Kölliker are fine fringes composed of an epidermis with polygonal cells; and of a homogeneous internal membrane, in which a simple network of capillaries uniting into two very small trunks is placed. In the skin of the back are found upon each side two longitudinal vessels, with whose termination M. Kölliker was not acquainted, but which appear to furnish branches for the penis also. Besides these vessels, M. Kölliker found under the microscope, in a fragment of skin with whose exact origin he was not acquainted, an oval tube which he considered to be decidedly a heart, but whose position he could not indicate. The generative organs are very much developed; they consist of a simple testicle, of an ejaculatory duct, and of a penis. The testicle is a transparent pyriform vesicle, which fills the whole of the abdomen of the *Hectocotylus*. In the interior of this vesicle there exists coiled up a fine cylindrical thread, without any proper envelope, and formed solely by filiform spermatozoa united together. Beside these spermatozoa, granular cells are found in very considerable number. This thread ends freely at its posterior extremity; but anteriorly it is continued forwards into the efferent canal which commences by a clavate extremity, folds back at first in the testicular vesicle, and finally passes into the penis. The efferent canal has a very peculiar structure, for its parietes are very solid, semi-transparent, yellowish, and composed of elastic fibres. The anterior part of the efferent canal is situated in the penis itself, and is traversed in its whole length by a spiral ligament, whose nature M. Kölliker could not determine.

M. von Siebold describes the posterior extremity of the *Hectocotyli* as a generative sac, in which the seminal mass, with the copulatory organ, and the efferent canal (provided with horny

tubercles in its interior, which are everted during copulation), which is continued into the penis, are contained. M. Kölliker describes these tuberculosities as little conical spines.

Besides the *Hectocotylus Tremoctopodis*, M. Kölliker describes and figures that of the Argonaut, which is distinguished from the former by the absence of branchiæ, of a sac-like abdomen, of a free penis, and by the presence of a filiform appendage which passes from the anterior extremity of its body. At the base of this appendage two triangular membranous lobes are placed.

The anatomical structure of this animal differs only in the structure of the filiform appendage and in that of the sexual organs. The filiform appendage is the continuation of the muscular tube forming the axis of the body. The testicular capsule is elongated and lined with pigment-cells, which are probably contractile. The testicle itself is formed by a spermatic thread coiled up, and surrounded by a structureless membranous envelope. The efferent duct leads into a silvery cylindrical tube, which is probably the penis, and which is certainly of a muscular nature.

M. Kölliker adds to this description of the *Hectocotyli* a long dissertation, in which he sets forth the opinions of his predecessors, as well as his own, the latter amounting to this,—that the *Hectocotyli* are the stunted males of certain species of Cephalopoda. "There is no need (he says) for any lengthy evidence that the *Hectocotyli* are independent animals. He who has not seen, as MM. Laurillard, Delle Chiaje, and I have done, their lively, independent, and continued movements, will not take them for portions of Cephalopods, and still less for spermatophora, if he considers their complicated organization, and if he calls to mind that they have a heart with vessels, branchiæ, nerves, and such well-developed generative organs." In the face of this positive assertion of M. Kölliker, we shall undertake to prove that the *Hectocotyli* are, however, nothing more than detached arms of Cephalopods, merely organized in a special manner.

After having shown that we were still unacquainted with the male of the Argonaut and with that of the *Tremoctopus*, M. Kölliker brings forward, first, the resemblance of structure between the *Hectocotyli* and the Cephalopoda; he finds that the suckers,

the chromatophora, and the muscular tube of the *Hectocotyli*, are constructed in exactly the same manner as the corresponding portions of the Cephalopods, and that they are met with exclusively among the latter animals. The presence of arteries and veins, of a heart, and of branchiæ, as well as the histological elements, are clearly opposed to the union of the *Hectocotyli* with the intestinal worms. Lastly, M. Kölliker relies upon the observations of Madame Power and of M. Maravigno at Catania, from which it would result that the *Hectocotyli* are formed as such in the egg, and that they then resemble a little worm, provided in its whole length with two series of suckers, with a filiform appendage at one of its extremities, and a little enlargement towards the other. From all this M. Kölliker concludes that the *Hectocotyli* are perfect animals ; and M. von Siebold has completely adopted this view, although this conscientious observer was able to discover neither the intestine nor the heart pointed out by M. Kölliker—essential organs, however, upon whose existence depends in great measure the opinion of these two naturalists.

In the meanwhile one of us had been employed in collecting, for many years past, materials which promised another solution of the problem. In his work upon the Cephalopoda of the Mediterranean, M. Verany relates, p. 128, that in 1836 he met with an *Octopus*, the description of which he published under the name of *Octopus Carena*. The captured individual possessed, instead of the right arm of the third pair, a vesicle seated upon a little pedicle provided with some acetabula. Upon many individuals collected after this period M. Verany observed, as of constant occurrence, that this same arm was always abnormally developed, and that most frequently the pedicle carried instead of a vesicle, a very large arm terminated by an oval globe, and having the form of the *Hectocotylus* of Cuvier. Our friend F. de Filippi, Professor at Turin, did in fact recognize this arm to be the *Hectocotylus*, M. Verany having submitted to MM. Filippi and Leydig (of Wurzburg), the latter a pupil of M. Kölliker, a specimen of *T. Carena* preserved in spirits of wine; this arm became detached by the least force, leaving a perfectly clean surface, whilst another arm could only be torn off by violence. The observers having opened the little terminal

sac, saw the white thread which terminates the *Hectocotylus* make its exit, like that of the Argonaut. M. Verany drew the following conclusions from these observations: "The *Hectocotylus* of the *Octopus* is only a caducous arm of the Cephalopod; this arm carries the male organs, and in all probability these organs are periodically developed. The *Hectocotyli* of the Argonaut and of the *Tremoctopus* differ from that of the *Octopus*. The *Hectocotyli* of the Argonaut and of the *Tremoctopus* cannot be the arms of the *Octopus* which carries them, since they are infinitely smaller, and since, so far as I am aware, these Cephalopods have never been found with an arm wanting."

Dr. H. Müller of Wurzburg visited the coasts of Sicily in 1850, with the intention of studying these contradictory facts. He communicated orally to one of us during his passage to Genoa, that having one day met with a very small Argonaut carrying a vesicle, he had taken this individual for an embryo still retaining its umbilical vesicle, but that on counting the arms he observed there were only seven, and that the eighth was replaced by this vesicle carried upon a little pedicle. Calling to mind the facts observed in the *Octopus*, Dr. H. Müller examined the animal which had come into his possession, and found that this little creature which he had taken for an embryo was in fact the perfect male of the Argonaut, and that the *Hectocotylus* was hidden within the pedunculated vesicle. We still await the publication of the observations collected by Dr. Müller.

As the foregoing extracts show, science has been loaded with a number of observations and opinions but little concordant with one another. Very desirous of obtaining a positive solution of a question which appeared to us to possess the highest interest, we united our efforts to procure a sufficiency of materials, and to study them during life. Fishermen were instructed by the one of us who could best make himself understood in the *patois* of the country, and the Cephalopods brought to the market in Nice were carefully scrutinized each day. The specimens, which were very rare, of Argonauts and Tremoctopods which fell into our hands, were the object of our minute but fruitless investigations. We could not find a single *Hectocotylus*, although one of us during a residence of two years at Nice examined seven Argonauts and three females of *Tremoctopus violaceus*.

We were in despair, when, in April of this year, the males of *Tremoctopus Carena* appeared all at once in very great numbers. We give in the following pages the results of our common studies, observing, however, that M. Verany especially occupied himself with the zoological portion, whilst M. Vogt principally took charge of the anatomical investigations.

I. *Zoology.*

TREMOCTOPUS CARENA. *Tremoctopus Carena*, Verany. *Poulpe Carena. Octopus Carena*, Verany. *Mém. de l'Académie Royale des Sciences de Turin*, 2e série, t. i. pl. 2.

Monographie des Céphalopodes de la Méditerranée, p. 34 & 128, pl. 14. figs. 2 & 3; pl. 41. figs. 1 & 2.

Body sac-like, provided with a constrictor apparatus. Head compressed; eyes large and projecting. Arms unequal: first and fourth pair longest. Acetabula pedunculated. Funnel very large; two aquiferous apertures.

Tremoctopus Carena, male (Pl. I. fig. 3. 4.).

Body sac-like, oval, slightly acuminated behind, very smooth. Branchial aperture wide, cleft as far as the orbits. Constrictor apparatus formed by a fleshy appendage having the form of an oblique hook, situate upon each side at the base of the funnel, and a horizontal cleft like a button-hole, in the thickness of the skin upon the internal margin of the body.

Head moderate, wider than deep, being compressed by the first pair of arms which arise at the level of the orbits; lateral part of the head occupied almost wholly by the orbits; inferior portion wholly covered by the funnel.

Eyes lateral; eye-balls projecting and flattened, wholly covered by a transparent membrane which is continuous with the skin; this membrane is pierced by a slightly contractile circular aperture, through which the crystalline lens presents itself wholly without covering.

Arms conico-subulate, unequal; the fourth pair is the longest and measures about two and a half times the length of the body; the first is shorter than the fourth and measures only twice the length of the body; the second is only half as long as the fourth pair; the left arm of the third pair is a little shorter than that of the second pair; the right arm of the third pair is hectocotyli-

form, and has a pedicle equal in size to the base of the arm of the opposite side; this pedicle carries a larger or smaller oval vesicle (Pl. I. f. 4.), containing the hectocotyliform arm or the perfectly developed *Hectocotylus* itself; this hectocotyliform arm is half as long again as the arms of the fourth pair. All the arms are provided with a double series of acetabula.

Acetabula:—these are large, cylindrical, much excavated, pedunculate, and distant from one another (Pl. I. fig. 3.); they alternate from the third, enlarge up to the sixth, and afterwards decrease progressively as far as the extremity of the arms where they are microscopic. The first pair of arms carries forty-five acetabula; the second, thirty; the third, thirty; the fourth, fifty.

The *Hectocotylus* is inserted upon a pedicle from which it is readily detached (Pl. I. fig. 3.); it is oval below and narrows towards its extremity, which appears as if truncated; the internal surface is flattened, and its whole contour is beset with a very close series of pedunculated acetabula which are oblique, *i. e.* have an oval section opening a little upon the inner side. These acetabula are united together by a longitudinal membrane which embraces the whole peduncle, and, with the acetabula, forms a continuous line by passing over at the base upon the inner surface of the arm. Generally a little ovoid sac terminates the *Hectocotylus*. This sac is transparent, and allows a convoluted cord to be seen through its membrane; the sac is frequently empty, and then the hectocotyliform arm is terminated by a filament or flabellum almost as long as the arm (Pl. I. fig. 3.), and which is its continuation. The *Hectocotylus* carries forty-seven acetabula upon each side. The dorsal part is a little convex upon its base; this convexity is markedly distinguished by a membranous sac open below (Pl. I. fig. 3.).

Interbrachial membrane rudimentary, absent between the lower arms.

Mouth surrounded by two lips, the internal ciliated, the external very delicate.

Funnel very large, extending far beyond the base of the arms, and measuring three-fourths of the length of the body. Two very large aquiferous apertures, placed at the base of the arms of the fourth pair at the point of attachment of the latero-dorsal portion of the funnel and communicating with the orbital cavity. Excluding the hectocotyliform arm, this Cephalopod is never

more than 0·110 (metre) in length; taking in this arm and its flabellum, it measures 0·220 (metre).

Colour.—During life this Cephalopod has a general transparency which allows the internal organs to be seen through the body, and in the lower parts, even the chromatophora which cover the membrane investing the organs of digestion and generation, and along the arms, the beaded nervous cord. When at rest, the body glistens with iridescent hues of azure, green and purple; the pupil is of a very brilliant burnished silver, and the dorsal portion of the orbits has a brilliant blue tint shot with a metallic golden tinge. The chromatophora are visible only with a lens, and have a purplish (*mauve*) tint passing into violet; when they dilate they are purple, and by the development of a great number of chromatophora the dorsal surface often passes into a velvety purple. When the creature is irritated or out of the water, the chromatophora take an orange-red tinge upon the lower portion; the points are constantly larger and more scattered than upon the upper. The funnel and the membrane which invests the eyes are equally covered with them. In spirit the chromatophora have always a wine-red colour; in a saline solution they retain their violet colour.

The *Hectocotylus* is wholly white, without chromatophora: the pedicle which carries it and the vesicle in its interior are covered with them.

Tremoctopus Carena, female.

Body sac-like, oval, smooth superiorly, very slightly tuberculated below. Branchial aperture and constrictor apparatus as in the male.

Arms conico-subulate, symmetrical; length as in the male. The first pair is provided with a longitudinal membrane upon its latero-superior portion, and the acetabula of the internal series are united together by a longitudinal membrane, as is observed also in the reticulated *Tremoctopus* and in the Argonaut.

Acetabula moderate, cylindrical, excavato-pedunculated, but little distant from one another; the first pair has eighty of them, the second seventy, the third sixty, the fourth eighty.

Interbrachial membrane, mouth, funnel, and aquiferous apertures as in the male.

Colour.—During life and in a state of rest the dorsal part of the animal is of a semi-transparent white colour, strongly shaded with blue; the inferior portion is white and very iridescent; the lateral parts of the body, of the head, of the dorsal portion of the inferior and latero-inferior arms, and the iris shine with a silvery lustre; the internal portion of the arms is of a pale rosy colour. In this state the dorsal portion is covered with microscopical chromatophora, and with others which are larger and regularly diffused, of a blue or violet colour; upon the lower portion of the body the chromatophora are disposed in the same manner, but their colour is violet passing into reddish yellow. The dorsal part of the body, of the head, and of the arms of the first pair assumes sometimes a very brilliant ultramarine colour, shaded with purple; sometimes this passes into a very dark velvety violet; the lower parts and the extremities of the arms are then coloured reddish yellow. Three different colours are often seen upon the back at the same time, and it is clouded with white, azure, rose-violet, yellow, and an infinity of dazzling shades produced by the mixture of these tints. Irritated, or in full vigour out of water, the animal covers itself wholly with reddish yellow chromatophora, but the dorsal portion is always strongly shaded with blue. Plunged in spirit, the skin of the lower part of the body becomes very finely reticulated, in consequence of the wrinkles formed by the subcutaneous granulated tubercles.

The male *Tremoctopus Carena* cannot be confounded with any of the known species; the proportions of the arms, and, above all, of the hectocotyliform arms, clearly distinguish it. The female closely approaches the reticulated *Tremoctopus* (*T. catenulatus*, Ver.), but the arms of *T. Carena* are much longer in proportion to the body, and the second and third pairs of its arms are comparatively shorter and less disproportionate to one another in size. The body is oval, while it is ovoid in *T. catenulatus*; finally, the tubercles are proportionally much smaller, more approximated and more numerous in *T. Carena*.

This Cephalopod appears only accidentally upon our coasts,—perhaps, as M. d'Orbigny thinks with regard to all the *Philonexidæ*, because it is pelagic; we have, however, met with it in all seasons, in February, April, September and December, which proves to us that it is a denizen of our latitudes. It is always

taken near land by means of drag-nets. Professor Bellardi of Turin, who was at Nice in April of this year, assured us that having been present at the raising of the *Madrague* nets*, he saw one of these Octopods attached to a dead *Salpa*. The *Octopus* evidently approaches the shore at the pairing season, and it is to this cause, as well as to the arrangements we made, that we owe the capture of twenty males and two females which were all taken last April. All the specimens have been brought to us living: a single male had lost its hectocotyliform arm; all the others presented this arm either wholly developed or still included within its vesicle. The male by itself has been described and figured since 1846 in the Acts of the Royal Academy of Sciences of Turin, by one of us, and later in the *Monographie des Cephalopodes de la Méditerranée* which has just appeared. The female has perhaps been described by M. Risso under the name of *Octopus tuberculatus*, but the short phrase applied to this new species is so vague and diffuse, that it may equally relate to the *Tremoctopus catenulatus*. M. Risso having left no specimen marked by himself by which it might be decided to which of the two species his description refers, we must retain the name given by one of us in 1836; and so much the more since M. d'Orbigny has already designated *Octopus tuberculatus*, another species of *Octopus* previously described by M. de Blainville.

M. d'Orbigny does not mention our *T. Carena* in his Monograph upon the Cephalopoda. It is very remarkable that this species, which this year was so frequently taken, and which besides does not appear to be very rare, should have escaped Delle Chiaje, who has enriched science with so many new species; Prof. Philippi, who has so carefully explored Sicily; M. Cantraine, who has traversed a large portion of the Mediterranean; as well as MM. Kölliker, Rüppell, Krohn, and H. Müller, who have specially occupied themselves with the Cephalopoda in Sicily. However, we have reason to believe that the *Octopus granulosus*, upon which Laurillard found the *Hectocotyli* which were described by Cuvier, is the female of the species with which we are engaged.

* Large nets employed in the tunny fishery, established permanently near St. Hospice, a league from Nice.

II. *Anatomy.*

We shall first treat of the anatomy of the male, whose organization in general does not differ, in fact, from that of other Cephalopods. The ventral region of the mantle is provided with a very complicated constrictor apparatus, fixed to the fibrous membrane which invests the intestine. After having cleft the mantle longitudinally (Pl. II. fig. 1.), we observe the branchiæ, each with a branchial heart situated at its base, and not differing in structure from those of other Octopods. During life, however, these branchiæ exhibited great contractility, and the branchial hearts, whose function has been questioned, pulsated regularly. The fibrous membrane which invests all the intestines is covered, especially below, with numerous chromatophora, which contract and dilate alternately. We see across this membrane the vaguely marked contour of the last portion of the intestine, of the ink-bag and of the genitalia which occupy the posterior portion of the body. The conjoint aperture of the rectum and of the ink-bag is placed upon a little muscular tongue which ends forwards in two very fine points, and which passes so far forwards below the funnel that the posterior edge of the latter covers it completely. At first we sought in vain for a long time for the aperture of the generative organs, which is perceived with great difficulty, when an accident discovered its position. One of the specimens which we were examining presented through the mantle a streak of white matter which began to fill the branchial cavity. Having carefully opened this individual, we saw a coil of the seminal thread, which we shall describe by-and-by, escape from a semilunar aperture upon the left side, by the side of the place where the branchial vessels leave the intestinal sac to pass into the branchia. It was afterwards easy to perceive this very much contracted cleft in all specimens, and to convince ourselves, by examining the internal generative organs, that this asymmetrical orifice was the sole means of discharging the contents of the generative organs into the branchial cavity.

After having taken away the fibrous intestinal sac (Pl. II. fig. 1.) we easily discover the rectum, which is very delicate, passes from below upwards from the dilatation of the large trunk, and which rises among a considerable mass of venous appendages

which especially invest the aortic heart and the great vessels uniting the latter with the branchiæ. Below this mass of venous appendages we see a flask-shaped organ of a gelatinous transparency, and through which fine silvery lines may be distinguished; these have a very peculiar lustre, and look like white lights painted thickly and with great brilliancy upon a grayish satin ground. These lines differ much in their arrangement in different specimens; we see, however, that they are especially numerous towards the posterior convex edge of the flask, whilst the anterior hollowed border of this organ seems to contain a more transparent substance. The bottom of the flask, whose form varies very much in consequence of the great contractility which it possesses, is turned to the right, while its narrowed neck passes to the left upon the great vessels of the branchia. This extremity hooks round these vessels, and at the summit of the curve is found the cleft orifice of which we have spoken above.

The remainder of the generative apparatus (Pl. II. fig. 4.) is situated upon the dorsal surface of the intestinal sac, and is continuous with the neck of the flask. It is composed of an elongated vesicle having nearly the same form as the flask, and possessing as great contractility in its transparent muscular parietes. It is divided into two portions, which however are united in a common envelope. The anterior portion we will call the cornu: it is membranous and transparent, and allows a contained whitish spiral thread to be seen through its side, much less brilliant and larger than the threads contained in the flask. At the posterior enlarged extremity of the cornu there is attached an organ having the form of a pointed apple, whose base is turned towards the cornu, its point towards the right branchia, with the heart corresponding to which it is in contact. This organ has a yellowish chalky tint; its internal surface is strongly attached by cellular tissue to the base of the flask; it is the testicle. The generative organs thus form altogether an actual ring (Pl. II. fig. 3.) round the great vessels of the left branchia; a ring which is completed behind only by the fibrous tissue uniting the envelope of the testicle to the bottom of the flask, whilst the closure of the ring in front, upon the ventral face, is produced by the union of the neck of the flask with the neck of the cornu.

We have just pointed out the form of the testicle; besides the general envelope which unites this organ to the cornu, it has a proper fibrous envelope which closely invests it. Invariably situated upon the dorsal surface, behind the branchial heart of that side, the testicle however changes its place more or less, according to the state of turgescence of the different portions of the sexual apparatus. The testicle itself is divided into two portions which differ in appearance even to the naked eye; the pointed extremity being more transparent than the body of the organ which is turned towards the cornu. Fine chalky lines radiate from the pointed extremity in all directions towards the enlarged centre of the organ, where they converge again to approach that face of the testicle which is in contact with the cornu. Under the microscope these chalky lines are seen at once to be the seminiferous tubes which end in a cul de sac at the pointed extremity of the testicle, and which begin to ramify when they enter into the thick portion of this organ. These ramifications however are almost parallel with one another, so that the entire testicle seems to be composed of parallel seminiferous tubes, which however converge both towards the point and towards the base of the organ.

The seminiferous tubes contained, in all the individuals we examined, no trace of completely developed spermatozoa, but only granular cells and very small free granulations, which from their strongly-marked contour had the appearance of fine drops of oil; the granule-cells also exhibited among the fine granules more strongly-marked little drops. All the individuals which we examined being in the pairing season, the spermatozoa had already passed into the ejaculatory organs, and in the seminiferous tubes of the testicle there were found only the elements required for the reproduction of the semen.

There is no direct connexion between the seminiferous tubes and the efferent canal; we have assured ourselves of this circumstance microscopically. The special envelope of the testicle (Pl. III. fig. 5.) is considerably narrowed at the base of that organ, and is directly continued into the muscular envelope of the cornu. A kind of funnel is thus formed at the place where the testicle is attached to the cornu, towards which all the seminiferous tubes converge to terminate by a rounded end. The contents of these

tubes ought then to be poured into the space formed by this funnel, which is nothing more than the continuation of the special envelope of the testicle. The seminal masses would, by means of this funnel, pass freely into the bottom of the cornu, if there were not a very narrow deferent canal (Pl. III. fig. 5 *a*), which is affixed to the funnel like a tube, and projects freely into the cavity of the cornu. Merely looking at the cornu, this canal may be seen applied to its dorsal surface; it is about 3 millimetres long; and even without opening the cornu, it is easy to convince oneself with a lens that its free extremity floats in the cavity of the cornu. This canal is extremely contractile and mobile, and has almost continually during life a vermicular motion. The structure of the canal is very simple: it is a muscular tube, with its longitudinal fibres especially developed, united into bundles and so forming slightly projecting ridges upon the internal surface of the canal. The orifice of the canal resembles the mouth of a hydroid polype, in consequence of these radiating ridges. The whole internal surface of the canal is covered with cilia of such large size, that the single ones can be distinguished with a magnifying power of 100 diameters, whilst the movement itself and the current produced by it are very distinctly visible by the very lowest powers. It is evident, from the disposition and structure of this efferent canal, that the seminal mass, entering the funnel in consequence of the rupture of the seminal tubes, is received by the efferent canal, and conducted by the latter into the cavity of the cornu, which thus in some respects serves as a seminal reservoir. *c*.

The structure of the cornu itself is very complicated, and we should have had considerable doubt as to certain points of its anatomy, if chance had not given into our hands many living animals in succession, upon which we were enabled to complete our researches. We have already mentioned the white and coiled thread which is visible across the transparent parietes of the cornu; this coil is constantly in motion, as well in consequence of its own contractions as of those of the investment of the cornu, which is very solid and is formed by muscular fibres interlaced in all directions. The coil is laid bare when this contractile envelope is cut open: it swims, so to speak, in a viscous liquid which fills all the cornu, and which glues together

all the folds of the coil, and that so effectually, that there is some difficulty in disentangling them. When the attempt has been successful, we see that the coil is obviously composed of two filiform organs rolled up together, *i. e.* of the deferent canal and of an accessory gland, whose excretory canal is united to the deferent canal towards the apex of the neck of the cornu.

The deferent canal (Pl. III. fig. 5 *d'*) begins by a trumpet-shaped orifice (Pl. III. fig. 5 *i*) folded like the orifice of the efferent canal, but wider than the latter; this orifice is not clothed with vibratile cilia, like the efferent canal, which tends to confirm our observation, that the two canals have no direct communication with one another. The plaited orifice of the deferent canal becomes continued into a considerable dilatation of a pear-shape (Pl. III. fig. 5 *g*) whose wider extremity is turned towards the orifice, while the tail a little enlarged passes into the continuation of the deferent canal; this dilatation is produced less by any enlargement of the cavity of the canal than by the very considerable development of the muscular layer, which forms very projecting longitudinal ridges at this place, converging towards the pointed extremity of the dilatation. Besides this greatly-developed muscular structure, we see, as an appendage to the pyriform dilatation, a perfectly rounded bag (Pl. III. fig. 5 *h*) which pours its contents by means of a little excretory duct, where the plaited orifice is continuous with the muscular dilatation. We could discover no histological elements in this secretion, which was composed of a substance resembling stearine.

The deferent canal is prolonged from the pyriform dilatation as a simple cylindrical canal. It possesses contractility, owing to a muscular layer which principally forms the tube. Two clavate enlargements succeed one another at a slight distance from the pyriform dilatation, and are owing, like the latter, to a greater development of the muscular layer. The interior of the deferent canal is clothed through its whole length with a glairy secretion, and most frequently the canal appears to be wholly empty; we however met with one individual in which a seminal mass was arrested before the first clavate enlargement. We shall return to this chance-discovery, since it throws some light upon the formation of the seminal machines in general.

In passing towards the pointed extremity of the cornu, the

deferent canal makes a multitude of folds, united to those of the accessory gland by very fine and very elastic fibres, which while they unite them, allow of a very considerable amount of contraction to each of these canals. At the extremity of the cornu the deferent canal opens into a kind of common reservoir which lies at the entrance of the cornu.

The accessory gland (Pl. III. fig. 5 *m*) which is enclosed in the cavity of the cornu, with the deferent canal, is composed of two portions, which, however, in their intimate structure present no essential difference—the gland itself and the excretory canal. The gland is a flattened body rolled almost spirally, and exhibits even to the naked eye a granulated appearance, resulting from the presence of many minute points which are almost entirely opake by transmitted light. The intimate structure of this gland is very remarkable; its parietes are very thick, and there is in the middle of the gland a cavity which is directly continuous with the excretory canal. Instead of glandular tubes, it consists of little, more or less rounded sacs (Pl. III. fig. 8.), which are hollowed in the very substance of the gland, and whose aperture is almost as large as its base. These sacs beset the whole internal surface of the gland and of its excretory duct; they are merely deeper in the gland than in the duct, and disposed a little more obliquely with regard to the axis of the gland. They are immediately surrounded by a very much developed elegant capillary network. The proper walls of these sacs are very thick; they are composed of a small number of circular fibres, and are lined internally with a considerable layer of cylindrical cells, carrying at their extremity very long cilia; these are in continual movement, and they transport a viscous homogeneous liquid containing fine granules, which are here and there united into little masses. These glandular sacs, which doubtless secrete the mass of which the envelope of the spermatic machines is formed, are continued until close to the anterior extremity of the excretory canal; there they disappear by degrees, and the excretory canal itself becomes considerably enlarged, to form a wide sac (Pl. III. fig. 5 *b*) into which the deferent canal also opens. This sac is on all sides attached to the parietes of the cornu, so that the cavity of the latter is completely shut at this place, and thus there is no other passage from the cornu to the flask than

through the sac. We see then, that in consequence of the very arrangement of the parts, the seminal masses carried by the deferent canal ought to meet in this common reservoir with the product of the secretion of the accessory gland, and to enter with it into the flask. It is probable therefore that here, in this wide sac with delicate walls, the spermatic machines are formed and pass afterwards into the flask.

The latter organ (Pl. III. fig. 1–4.) is situated, as we have already said, upon the ventral face of the intestinal sac immediately under the fibrous envelope which surrounds the latter. The membrane which forms the flask is very delicate, very contractile, and almost impermeable to water. In its interior we see undulating brilliant white lines, such as we have described above, and which are sometimes so obvious that they might be taken for external ornaments of the envelope. The semilunar aperture situated close to the neck of the flask is generally very difficult to perceive, and opens only after a prolonged stay in the water to give exit to the contents of the flask, which are formed in all the individuals we have examined by a unique spermatic machine,— by a single spermatophore filling the whole cavity so completely, that it is very difficult to open the latter without damaging the spermatophore contained in its interior.

This enormous spermatophore (Pl. IV. fig. 1.), which is nearly two centimetres in length, is always folded up in the flask, so that both its extremities approach the semilunar aperture of the latter. Removed from the flask the spermatophore has the shape of a powder-horn, having one extremity pointed and elongated into a beak, the other enlarged and rounded. The beak, although the more firm and consistent portion, is however almost transparent, whilst the sac appears almost white, by reason of the convoluted silvery thread which it contains in its interior. The spermatophore itself is formed by a very solid membrane, perfectly transparent, which, after having formed the sac, is continued upon the beak-like prolongation, surrounding it very closely. This envelope absorbs water very quickly, and swells out rapidly in consequence; it becomes separated then into two layers, the exterior of which, very delicate, forms irregular folds, often so multiplied that one might imagine the beak of the spermatophore to be constituted here and there by the convolutions

of a fine spiral thread. The proper coat which lies below this layer becomes distended by the action of water, very much as a gummy mass would be, and finally bursts to allow the passage of the contents of the spermatophore.

These contents are composed of two very dissimilar threads; the one belonging especially to the beak-like prolongation, the other to the sac of the spermatophore. We call this last thread the spermatic cord (Pl. IV. fig. 2 *c*), since it is wholly made up of spermatozoa united together around a fine thread-like axis. This spermatic cord is entirely white, silvery to the naked eye, and of an even diameter throughout, except its anterior extremity, where it becomes more delicate, to attach itself finally by an excessively delicate thread to the posterior extremity of the ejaculatory cord. The spermatozoa are united together in the spermatic cord in such a manner that their cylindrical end, which is the larger, is attached, or rather glued by a viscous liquid, to the axis of the cord, whilst their very fine caudal extremity is turned towards the periphery. We can compare this structure to nothing better than to the elongated brushes used for cleaning bottles, in which the bristles radiate upon all sides from a median axis formed by an iron thread. The spermatic cord becomes distorted very soon when it is subjected to the action of water, and it is almost impossible to unroll its coils before the completion of this distortion. At the very moment the spermatic cord is drawn out of its envelope, all the spermatozoa appear to be united by a glutinous liquid, which connects them so closely that it is impossible to distinguish them. By the action of water, this glutinous mass at first dissolves a little; the spermatozoa become free, and appear then to be animated by slight undulatory movements. Little by little these motions cease, whilst the glutinous matter congeals by the operation of the water, and to such an extent that the spermatic cord soon looks like a felted mass whose elements are undistinguishable. It seems probable to us, that the irregularly nodulated appearance noticed by Von Siebold upon the spermatic cord of the *Hectocotylus Tremoctopodis*, proceeds from a similar alteration produced by the influence of water.

We have said that the spermatic cord ends by a more delicate extremity, when, forming numerous convolutions, it approaches

the anterior extremity of the sac, where the beak-like projection of the spermatophore commences. In fact, the cord becomes very delicate (Pl. IV. fig. 3 *a*), and finally attaches itself to the posterior extremity of the ejaculatory canal, which in its turn fills the beak-like projection of the spermatophore. This ejaculatory canal is formed by a very firm tube with thick parietes, having only a very small canal in its interior. Its parietes are excessively transparent, resist pressure greatly, and do not become disfigured by the action of water. We have been quite unable to discover any further structure in this homogeneous tube, which commences in the sac of the spermatophore by a rounded extremity, slightly drawn out, and having a minute aperture into which the extremity of the axis of the spermatic cord penetrates as a very fine thread repeatedly folded up in the cavity of the ejaculatory canal. The latter widens very soon, together with its internal cavity, which is filled in the whole length of its course by a spirally folded membranous ligament. We see distinctly in the posterior extremity of the ejaculatory cord the commencement of this membrane, which clothes the interior of the canal of the cord, and seems at first plaited into a number of transverse folds, which by degrees assume a spiral disposition, so that at last the end of the ejaculatory canal resembles under the microscope the intestine of a shark with its spiral valve (Pl. IV. fig. 4.). The ejaculatory canal forms at first many folds in the wider portion of the beak-like prolongation; after which it becomes continued almost in a straight line, forming itself the axis of the prolongation. At the extremity of this prolongation may be distinguished the whole external envelope of the spermatophore, which becomes bent back, so to say, towards the interior to form the tube of the ejaculatory cord, whose canal, clothed by the spiral membrane, is continued as far as this extremity.

The analogy between the structure of the spermatophore which we have just described and that of those of the other Cephalopoda with which we have long been acquainted is evident, so that we need insist at no greater length upon this point. The envelope which swells out by the action of water; the ejaculatory cord, with its internal spiral ligament; in all these points the resemblance is complete, with this difference only, that the semi-

nal mass is not included in a sac as in the other Cephalopoda, but is formed by a long cord coiled upon itself and completely deprived of any special envelope. The formation of these seminal machines, whose size is enormous relatively to that of the male animal, is pretty well explained by an observation we made upon one of the four individuals which we examined. A whitish mass (Pl. III. fig. 5 *f*) was situated in the deferent canal of this individual a little beyond the pyriform enlargement by which this canal commences. It presented itself under the form of a pear (Pl. III. fig. 9.) with an elongated tail, containing internally a thousandfold coil of a fine gelatinous, very transparent thread, beset on all sides with motionless spermatozoa. This thread became lost by degrees in the more enlarged portion of the mass; and even by pressing aside the matted spermatozoa forming it, one could only distinguish here and there some traces of a similar gelatinous thread; it was however by no means well marked. This mass of spermatozoa was not invested by any envelope, and it still retained the form of the foot-like enlargement in which it had been modelled. It seemed evident to us that such a seminal accumulation is moulded by passing through the whole length of the deferent canal into an elongated thread, and that it is in the common reservoir that this thread receives at once both its envelope and the ejaculatory cord secreted by the accessory gland, which thus transforms the whole into a spermatophore. This, once formed, passes into the flask, whence it is expelled when copulation is about to occur.

In the great majority of individuals which we examined, the right arm of the third pair was disproportionately developed, and had an external organization such as we have pointed out in our zoological description. In other individuals this arm was replaced by a very considerable pedunculated vesicle. We shall see by the anatomy of these parts that there exists a correlation between them—an intimate correlation—and that the formation of the vesicle must necessarily precede that of the hectocotyliform arm.

As to the latter, we have been unable to discover in its structure any great differences beyond those we are about to point out, from that of an ordinary Cephalopod-arm. The axis of this arm is formed by a cylindrical muscular tube of great thickness,

which is continued beyond the series of acetabula into a long filiform appendage which we name the "flabellum," and which is ordinarily concealed in an ovate sac which terminates the anterior extremity of this arm. This muscular axis is formed, as M. Kölliker has already very well shown, of three different layers, one of which is longitudinal and the other two circular. In the midst there is a hollow cylindrical space, in which are situated two organs which require the more careful examination, since M. Kölliker has entirely mistaken their nature. One of these organs is a blood-vessel with very delicate and transparent parietes, which runs through the whole length of the muscular axis even in the portion which we have called the flabellum, without any great diminution of its volume. There can be no doubt as to the exact nature of this vessel, which we have many times observed by transmitted light in individuals still living, but in which the movements of the heart were too irregular to allow of our determining the direction in which the current of the blood moved. We could very well distinguish the blood-corpuscles, forming at the time of death irregular masses, which, while the heart yet beat, were agitated more or less distinctly. Unable to make any injection of the few specimens at our command, we could not correctly determine the relations between this vessel occupying the central axis of the muscular cylinder, and the cutaneous vessels which appear upon the whole surface of the arm. We believe, however, that we have seen, towards the anterior extremity of the flabellum, this central vessel giving off lateral branches, which pierce the muscular tube to pass to the external surface and to the skin. The vessel is continued uninterruptedly into the pedicle of the arm, where we were unable to trace it further. It seems indubitable, however, after what we have just said, that it is the central artery of this abnormal arm, disposed like the central arteries of the other normal arms.

The second organ worthy of remark, and which is enclosed in the muscular canal, is the nervous cord formed by as many ganglia as there are acetabula upon the whole length of the arm. The tissues of the living individuals are so transparent, that we can perfectly well distinguish the nervous cord in all the arms of these little males without any dissection, and all the ganglia

corresponding to the acetabula can be counted with the most scrupulous exactness. It is equally easy to see this ganglionic cord in the hectocotyliform arm, and to decide that, as M. von Siebold has well observed, there is only a single ganglion corresponding to each acetabulum; but the acetabula being very closely approximated, and succeeding one another alternately upon the two sides, the ganglia also are pressed against one another, so that to the naked eye, or under a simple lens, they look like the close beads of a necklace. Examined microscopically, these ganglia (Pl. IV. fig. 6 *c*) all show the form of a trapezoid whose base is turned towards the acetabulum to which the ganglion belongs. M. Kölliker has figured the appearance of these ganglia pretty well; but by an inconceivable mistake, he regards the ganglia as masses forming the contents of the central vessel which he makes out to be an intestine. The nerves passing from these ganglia are to be seen with great difficulty, inasmuch as they penetrate the muscular cylinder in such a manner that they are almost always perpendicular to the microscope. Hence M. Kölliker has described these nerves as canals ascending towards the surface of the skin; and we must confess in fact, that a little nerve viewed perpendicularly upon its axis is not unlike a fine canal with delicate sharp parietes.

The chain of ganglia ends with the series of acetabula; but some nervous threads which are very delicate might yet be perceived in the muscular axis of the flabellum, where they ended by becoming so fine that it was impossible for us to trace them to its extremity.

We find no differences whatsoever in the structure of the rest of the arm, so far as there are suckers; the skin, the walls of the acetabula and their whole structure appear to be entirely conformable with all that we have seen in the arms of ordinary Cephalopods: we may be allowed then to pass over these points in silence.

The anterior extremity of the arm is formed by a little oval sac, which hangs between the two last acetabula, and whose wall is a direct continuation of the skin which covers the dorsal face of the arms. On carefully examining this little sac, we perceive even with the naked eye that its interior contains a spirally coiled thread. Between the two last acetabula there exists

a little fissure which leads into the cavity of this sac, and by which the animal is enabled to evolve the spiral filament hidden in its interior. We have frequently seen instances of this occurrence; the filament passed by its pointed extremity out of this cleft and slowly unrolled itself; the sac all the while being agitated by repeated contractions which aided the expulsory movement. The filament itself performs very marked vermicular movements, which we can only compare to the motions of the tentacular filaments of certain tubicolar worms, particularly of the *Terebellæ*. The little sac is wholly contracted when the thread has passed out of it, and it then exhibits under the microscope (Pl. IV. fig. 6 *e*, *f*) very numerous rugosities, presenting a sort of very pretty watered pattern. It evidently consists of two membranes, one external, which is nothing more or less than the continuation of the skin which covers the whole arm, and an internal muscular layer which is continued by two muscular bundles upon the two sides of the flabellum. This sac contracted upon the flabellum, which it had contained, has been also seen by the authors who have written upon the *Hectocotylus* of the *Argonaut*; and lastly by M. Kölliker, who regards it as a membranous appendage without any other signification.

The flabellum itself (Pl. IV. fig. 8) is composed especially, as we have said above, of the muscular cylinder of the arm, which occupies its centre without interruption as far as its extremity, gradually becoming smaller. This cylinder ends by a point at the very extremity of the flabellum, which is at first completely rounded, but becomes flattened little by little like a lance-head towards its end. At the distance of a few millimetres from the extremity of the flabellum the muscular cylinder becomes suddenly thickened, and takes the form of a piston (Pl. IV. fig. 8 *b*); its internal cavity even is here widened. At this same place we have always seen a considerable mass of blood-corpuscles distending the enlarged cavity. The median vessel which occupies the centre of the muscular tube, ends therefore here in a kind of reservoir, whilst the muscular axis continues as a hollow cylinder as far as the extremity. The external membrane which invests the flabellum is, especially at its base, very loose, and exhibits proper undulatory movements due to two muscular bun-

dles which run along the two sides of the flabellum, and which may be followed even beyond the piston-like enlargement. These two cutaneous muscles are accompanied through their whole length by two venous trunks which send off numerous ramifications, forming a capillary network over the whole surface of the flabellum. These ramifications are especially remarkable at the very extremity of the flabellum, where they are perceived very easily, the tissues being at this place completely transparent.

The extreme mobility of the flabellum perhaps plays a part in the physiological functions of the hectocotyliform arm. We have seen this appendage continually in movement, as if it were feeling about to fix itself somewhere. It embraced the arms, and even the body of the animal to which it belonged, but it disentangled its coils again without its being possible to discover to what end all these motions tended. We shall bring forward by-and-by an observation of M. Kölliker's, which will, perhaps, set other observers upon the track of the physiological function of this part.

We have yet to mention a last peculiarity of the structure of the hectocotyliform arm; it is the existence of a sac of considerable extent, which is visible upon the posterior or dorsal face of the arm near its base, and therefore opposite to the acetabula. This sac (Pl. I. fig. 3 *a*) is 15–20 millimetres in length, and is elongated, inasmuch as it lies along the dorsal face of the muscular cylinder of the arm. It is distinguished very easily throughout its entire extent by its deep colour, whilst the rest of the hectocotyliform arm is wholly colourless. This coloration is due to the chromatophora which beset the whole internal surface of the sac, and may be seen shining through it. A semilunar aperture, situated upon the dorsal face of the arm immediately above the pedicle, leads into this sac, which is a true culde-sac, and is closed upon all sides. We have never found anything in this sac, which is obviously a diverticulum, an involution of the skin of the body itself, and whose formation depends, as we shall soon see, upon the mode of development of the arm.

We have already many times mentioned the oval vesicle carried upon a delicate pedicle, which was observed in many individuals in the place of the hectocotyliform arm. Upon closely examining this vesicle, we see that it is lined in its whole extent

with the same chromatophora as those which are distributed over the whole surface of the body, and that it has at its base a little semilunar aperture similar to that which we have observed in the sac of the arm. Upon opening the vesicle we find in its interior the hectocotyliform arm coiled up spirally (Pl. IV. fig. 7), so that its acetabula are turned towards the centre; the dorsal face of the arm towards the periphery of the vesicle. This arm had reached its full development in the individuals in question; but in these also the vesicle had attained its final stage of development, since it is much smaller in a specimen described by M. Verany in his work already quoted. Whilst we were examining the arm rolled up in its vesicle, another living individual placed in sea-water unrolled little by little the arm concealed within its vesicle. The arm passed out by its base, and whilst it kept on unrolling, the vesicle was reversed by the same action, and ended by becoming the sac which we have described upon the dorsal surface of the arm. It will now be readily explicable why this sac has its internal face lined by chromatophora similar to those of the skin, the external surface of the vesicle having become the internal face of the sac. We can now also account for the fact, that in all the individuals we observed the hectocotyliform arm was always twisted and rolled up at its extremity, an arrangement which was a result of the spiral coil which it had formed in the vesicle.

We may be very concise in our description of the female organs, which are constructed upon the same plan as in *Argonauta* and *Tremoctopus*. The simple ovary surrounded by its capsule is situate at the bottom of the intestinal sac, and communicates with two very long and convoluted oviducts, which are folded up upon the two sides of the ovary. There does not exist, as in *Tremoctopus violaceus*, any decided glandular enlargement in the course of the oviducts; but in the sole female which we have had an opportunity of examining, we found in the course of the left oviduct two eggs of an oval form, which were still retained in the oviduct, and which were evidently on their way out. The two apertures of the oviducts are placed as in the two other species of Octopods which have hectocotyline generation, (i.e. *Argonauta* and *Tremoctopus violaceus*,) at the base of the branchiæ; the oviducts passing under the branchial arteries and veins to

open by two little lateral papillæ into the respiratory cavity. These apertures are very distant from the funnel, and are placed altogether at the sides of the cavity.

The investigations which have been set forth in the preceding pages ought, we think, to furnish a very complete solution of this important question concerning the nature of the *Hectocotyli* which has been agitated now for some years. Accepting the results of MM. Siebold and Kölliker, and the conclusions which they drew, one was still struck by a something surprising and in strange contradiction with certain zoological principles which were believed to be firmly established. Among these Cephalopods—so similar for the rest in their external and internal structure—there were, according to this view, to be found kinds which could hardly be distinguished generically, and yet in which the difference between the organization of the male and that of the female was carried to its greatest extent. According to this view, females endowed with all the complicated and highly developed organs of the Cephalopoda possess males which previous observers had taken for intestinal worms, and which in any case were so poorly organized that independent life seemed refused to them; and so strange an exception, an example of which is hardly to be found in the animal kingdom*, was to be found in species side by side with others, in which the males were organized as completely as the females. It was evidently a question which ought to be in the highest degree interesting to zoologists, and we are rejoiced to believe that the solution we offer, and which we believe to be definitive, will not remain without influence in preventing for the future similar mistakes.

It would be useless to reiterate this truth, that the being discovered by Laurillard at Nice, and described by Cuvier, is really the detached arm of that species of *Octopus* which we call *Tremoctopus Carena*, and that the individuals which carry these deformed arms are always the males—smaller it is true than the females—but for the rest organized in as complete a manner as the other Cephalopoda. We have thought it superfluous to

* The *Entomostracous Crustacea*, the *Rotifera*, and the *Cirripedia*, classes which present instances of disproportion between the sexes quite as remarkable as Kölliker supposed it to be in *Argonauta*, &c., seem to have been forgotten by MM. Verany and Vogt.—*Tr.*

give any detailed description of the nervous, alimentary, circulatory, and respiratory systems of these animals, the high organization of these systems being obvious from our figures or from the mere inspection of the animal. It is the same for the male of the Argonaut, although the difference in shape between this and its female is still more remarkable; so great indeed, that so scrupulous an observer as our friend M. Krohn neglected to examine these little creatures, which he took to be young just hatched, and still provided with their yelk-sac. We have already said that the discovery of these minute males of the Argonaut belongs to Dr. Müller of Wurzburg, who will without doubt inform us that their internal organization resembles that of the other Cephalopoda. We have only been able to examine a single specimen of these minute males, long preserved in alcohol, and given to one of us by M. Krohn, and we can affirm that in point of external structure, which we have alone examined, it perfectly agrees with the type of the other Cephalopods. This is obvious from the figure we have given of this little male*. The male of the *Tremoctopus violaceus* alone is not yet known; however, we have no fear but that further researches, in the direction we have taken, will discover the male which bears the *Hectocotylus* described by M. Kölliker, and which differs in many points from the other *Hectocotyli*.

All the *Hectocotyli* that have been described up to the present time as perfectly independent beings are then nothing else than the detached arms of certain species of Cephalopods, in which the males, for the rest perfectly normal, are smaller than the females. All our observations prove that these arms are detached with extreme readiness, and that the pedicle which carries them exhibits, after its separation, a clean smooth surface, without any trace of laceration. The detached *Hectocotyli* prove as evidently that this separation takes place in a natural manner, for their posterior extremity never exhibits any trace of tearing nor of cicatrization. The pedicle which remains upon the body after the arm has become detached, without question reproduces this arm, and that probably by a process of budding, comparable perhaps to the reproduction of the deciduous horns of certain ruminants. Our observations have only permitted us

* Omitted here.—*Tr.*

to make out the last phase of this reproduction, when the abnormal arm, coiled up in a spiral, is enclosed within a vesicle, from which it ought soon to make its exit and unroll outwards. But it seems to us unquestionable that the arm is really reproduced in the interior of this vesicle, by budding from the peduncle and raising up the skin covering the latter, which thus in the end forms the vesicle enclosing the arm. The vesicle which the little male of the Argonaut carries has exactly the same relations; it also contains in its interior the spirally coiled *Hectocotylus*.

Our observations as they stand could furnish only very scanty indications as to the physiological function of these abnormal arms of the males; we have found in fact in these arms only the ordinary structure of a cephalopod-arm terminated by the flabellum—a kind of tail fixed to one of the extremities,—and by a cutaneous sac at the other extremity. This sac was invariably empty in the individuals in which the arm was still fixed upon its pedicle; it is formed, as we have just seen, by the retroversion of the sac in which the arm is developed. But our investigations, combined with the results obtained by MM. Cuvier, Laurillard, Kölliker, and Siebold, solve the problem. All these observers have examined the *Hectocotyli* when detached; all have noticed that in these separated individuals the sac situated at the base was by no means empty, but that it was filled by organs belonging to the generative apparatus. MM. Kölliker and Siebold have also determined that this sac contains a long folded spermatic cord, which is continued into an ejaculatory canal, having a harder pointed extremity, which these writers call the penis, inasmuch as they believe the full sac and its contents to be a true testicle, with the excretory and copulatory canals, which are ordinarily in connexion with this organ. Now, our observations are formally opposed to this interpretation. We have proved in fact that the testicle is situated at the bottom of the intestinal sac, and that it is constructed upon the same type as that of other male Cephalopods. We have shown besides, that this testicle is in relation with the peculiar excretory organs which fashion the seminal mass, so as in the end to form a seminal machine—a spermatophore—of a very complicated structure and of very considerable dimensions.

Now that we have exactly described the spermatophore contained in the flask, let any one compare our description with that which MM. Kölliker and Siebold have given of the contents of the sac of the *Hectocotylus*, and the perfect agreement of the two will be obvious: the spermatophore surrounded by a transparent envelope, having the same properties as the envelope of the supposed testicle in the *Hectocotylus*: the seminal cord of the spermatophore resembling in all respects the same organ rolled up in the genital capsule of the arm: the ejaculatory cord of the seminal mass with its spiral ligament, its more solid and pointed extremity, nowise different from the deferent canal and the penis described by these authors;—there can no longer be any doubt as to the identity of these organs. It is then evident that the seminal machine constructed in the internal organs of the male, leaves these organs to be transplanted into the sac which the hectocotyliform arm carries; this then, loaded, becomes detached from its pedicle and affixes itself to the female, in all probability during an act of copulation or embracing, which takes place, as we know, among the other Cephalopoda.

It is true that no observation at present known explains to us the mode of transport of the seminal machine from the aperture of the generative organs situated in the branchial cavity as far as the sac of the abnormal arm; and it may be that the mobile flabellum which terminates the *Hectocotyli* of the Argonaut and those of our *Tremoctopus Carena*, is charged with the performance of this removal of the seminal machine. M. Kölliker has observed, in fact, that in one specimen of the *Hectocotylus Argonautæ*, the anterior extremity of the flabellum was bent back into the aperture of the sac containing the seminal machine, and that this extremity was twisted around the machine. It may be that M. Kölliker surprised the *Hectocotylus* at the moment when the flabellum was depositing its seminal mass in the sac of the arm, though it is very possible on the other hand that this engagement of the extremity of the flabellum was simply an accident due to the continual explorations performed by the organ. The acts of copulation and fecundation even are not yet known to occur by direct observation; but as all the observers who have up to this time found detached *Hectocotyli* have found them on the arms, in the funnel, and in the respiratory cavity

of the females, it is probable that these charged arms creep by the aid of their numerous suckers as far as the aperture of the female generative organs, when the spermatophore then performs its office.

We sum up then by offering the following conclusions:—

1. The *Argonaut*, the *Tremoctopus violaceus*, and *T. Carena*, have males whose structure agrees with that of the common Cephalopod-type.

2. One of the arms of these males becomes specially modified into a copulatory organ.

3. The beings known at present under the name of *Hectocotyli* are not separate animals, but are merely the detached copulatory arms of the males, charged with a seminal machine.

4. The copulatory arms are detached and renewed periodically.

DESCRIPTION OF THE PLATES.

[The great number of figures given by MM. Verany and Vogt rendered it requisite to exercise some selection, and to exclude any that were not absolutely necessary. Of their four Plates, the three last (Pl. 7, 8, 9, *Annales*) are exactly copied in our Plates II. III. and IV.; but only two figures of their first Plate (6, *Annales*) are given in our Plate I. figs. 3, 4. The others appeared to be not necessary to the comprehension of the memoir. This change has of course rendered requisite a new numbering of the figures.]

PLATE I.

Fig. 3. *Tremoctopus Carena*. Male, seen from the dorsal surface. *a*, aperture of the retroverted sac which contained the *Hectocotylus*; *b*, vesicle which contained the flabellum; *c*, flabellum.

Fig. 4. *Tremoctopus Carena* (male), with the vesicle still containing its *Hectocotylus*.

PLATE II.

Fig. 1. Male *T. Carena*, seen from the ventral surface. The visceral sac is cleft longitudinally, and the left half of the mantle has been thrown back to exhibit the branchia and the aperture of the male organs at the moment of expulsion of the spermatophore. *a*, funnel; *b*, vesicle containing the *Hectocotylus*; *c*, eye; *d*, aquiferous aperture; *e*, mantle; *f*, branchia; *g*, branchial heart; *h*, flask; *i*, spermatophore passing out.

Fig. 2. The same. The mantle is cleft and thrown back, the funnel is taken away; the fibrous envelope of the abdominal cavity is cut so as to

exhibit the organs in their natural position. The letters *a*—*h* have the same signification as before. *i*, abnormal arm, *i. e.* the *Hectocotylus*; *k*, the anus; *l*, the rectum; *m*, the large intestine; *n*, the ink-bag; *o*, the ventral aorta; *p*, the venous appendages.

Fig. 3. The genitalia with the branchiæ, the hearts, and the large intestines, wholly detached and seen from the ventral side. The letters as in the foregoing figures. *q*, cornu; *r*, testicle; *s*, aortic heart.

Fig. 4. The abdominal organs seen from the dorsal side. *t*, stomach; *u*, cæcum; *v*, liver; *w*, dorsal aorta.

*** These four figures are twice the natural size.

Fig. 5. Abdominal organs of the female *T. Carena*, seen from the ventral side. Natural size. The mantle is thrown back; the fibrous envelope of the abdomen is taken away: for the rest the organs are in their natural position. *a*, funnel; *b*, anus; *c*, branchiæ; *d*, branchial hearts; *e*, venous appendages; *f*, sexual apertures; *g*, ovary.

Fig. 6. The sexual organs isolated, seen upon the ventral surface and magnified twice. *a a*, oviducts; *b*, ovary; *c c*, ova passing along the oviduct.

PLATE III.

Figs. 1—4. The male sexual organs magnified 2 diam. completely detached and viewed (figs. 1 & 3) from the ventral side, and (figs. 2 & 4) from the dorsal side. *a*, flask with the aperture and the spermatophore; *b*, cornu; *c*, testicle with the efferent canal.

Fig. 5. The cornu is open for its entire length. The deferent canal and the accessory gland are unrolled. *a*, continuation of the cornu into the neck of the flask; *b*, common reservoir; *c*, aperture of the deferent canal; *d*, aperture of the excretory canal of the gland; *d'*, deferent canal; *e e*, clavate enlargements; *f*, seminal mass contained in the canal; *g*, pyriform enlargement; *h*, globular gland; *i*, aperture of the deferent canal; *k*, envelope of the cornu; *l*, excretory canal of the accessory gland; *m*, accessory gland; *n*, efferent canal; *o*, envelope of the testicle; *p*, testicle.

Fig. 6. Contents of the seminiferous tubes. × 400.

Fig. 7. Structure of the efferent canal.

Fig 8. Glandular sac of the accessory gland. × 400. *a*, capillaries.

Fig. 9. Seminal mass contained in the deferent canal. Posteriorly, only the contour of the felted spermatozoa and the traces of the developing transparent thread are indicated. *a*, transparent thread.

PLATE IV.

Fig. 1. Spermatophore withdrawn from the flask.

Fig. 2. The anterior extremity of the same, considerably magnified and viewed by transmitted light. *a*, transparent envelope; *b*, ejaculatory cord; *c*, seminal cord.

Fig. 3. Posterior extremity of the ejaculatory cord in connexion with the seminal cord. *a*, seminal cord; *b*, fine membrane applying itself to

the envelope of the spermatophore; *c*, posterior extremity of the ejaculatory cord; *d*, commencement of the spiral membrane.

Fig. 4. A portion of the middle of the ejaculatory cord. *a*, tube of the cord separated into two layers; *b*, spiral membrane.

Fig. 5. Anterior extremity of the spermatophore.

Fig. 6. Extremity of the acetabuliferous portion of the hectocotyliform arm, with the commencement of the flabellum and the entrance of the sac. *a*, flabellum; *b*, muscular cylinder of the flabellum continued into the arm; *c*, nervous ganglia; *d*, acetabula; *e*, external layer of the sac; *f*, internal layer of the sac.

Fig. 7. The vesicle opened to show the abnormal arm coiled up in its interior. × 2.

Fig. 8. Anterior extremity of the flabellum. *a*, muscular cylinder; *b*, clavate enlargement.

Fig. 9. Part of the middle of the flabellum, considerably magnified. *a*, central vessel; *b*, parietes of the muscular tube; *c*, skin enveloping the flabellum; *d*, lateral cutaneous muscles; *e*, cutaneous vessels.

[T. H. H.]

Article VI.

Organographical Observations on certain Epigynous Monocotyledons. By H. Crüger, of Trinidad.

[From the *Linnæa*, vol. xxii. 1849.]

THE development of the natural sciences from the time when they first began to merit the name, may be divided into two principal periods, according to the directions taken by research. In the first, the object was the distinction of natural bodies from each other, and the formation of what is called the systematic part of science. After a body of facts had been brought together, inquirers, acquainted with distinctions, began to seek for analogies, and thus more philosophical views respecting the kingdoms of nature came gradually into existence. The Artificial Systems date from the first epoch, the Natural Methods from the second. While the aim of systematic science is division, that which searches for analogies endeavours to combine, partly to facilitate the comprehension of the whole, partly in order to discover the laws prescribed for the formation of bodies. Both branches of science are immeasurable, and a lifetime is insufficient for a tolerable mastering of only one of them.

One of the difficulties which especially oppose the acquirement of an accurate knowledge of plants, is the circumstance that certain parts of the globe possess peculiar forms which can be obtained only at great cost and with much trouble in distant zones. And here it is that descriptive botany has far outstripped the branch to which this essay is devoted, although it cannot be denied that much has already been done in this. Since I have command here in Trinidad of abundance of material for the investigation of tropical plants, I may perhaps be permitted to contribute the following, towards filling up a gap in special botany.

The group of *Monocotyledoneæ epigynæ*, comprising the Scitamineæ, Musaceæ and Orchideæ, is distinguished by certain common characters from the other families of this division of

the vegetable kingdom. Among these are the irregularities of the parts of the flower, which have occupied the attention of morphologists for some length of time. To these must be added the high degree of development of the leaves, which in the Musaceæ and Scitamineæ are separated from the petiole by a very evident, swollen articulation, and which goes so far in most of the Orchideæ that the leaf becomes detached from its stalk at this place. If, with Lindley, we exclude the Dictyogens as a transitional class, this structure recurs in the Endogens only in the Aroideæ,—in some of which the leaf falls off its stalk when old, while others present real compound leaves, and in the Grasses, which approach not a little to the Scitamineæ in this particular in such genera as *Pharus*, and in which the petiole and lamina are most evidently distinct. These forms of leaf, it may be remarked in passing, prove how mistaken those botanists were who ascribed a *folium petiolaneum* to the Endogens generally.

In most of the plants of the three families above named, with which I am acquainted, it is seen at once that in those genera in which the stem produces branches, the inflorescence is very compound, and on the other hand, that where branches are only produced on a subterraneous stem, the inflorescence likewise remains pretty simple. To what extent this may be generalized is a question I must leave to the decision of those who have access to a large number of species, in collections, &c. In the following pages will be found, where requisite, a short description of the parts of the flower of certain plants of these groups, together with a fragmentary contribution to the history of their development.

Musaceæ. *Heliconia Bihai*, Sw.—The accompanying diagram (Pl. V. fig. 1) illustrates the relative position of the parts of this flower. I must remark, that the generic character, as I find it given by Endlicher and others, does not agree accurately with the species of *Heliconia* with which I am acquainted here, and we possess five in Trinidad. The two lateral, external, and the three inner petals are more or less coherent, the outer petal next the axis is free, and the stamen in front of this is abortive.

The inflorescence of this species is composed of a number of abbreviated flowering branches which are attached to the rachis

alternately in two rows, enclosed in large bracts. The individual flowers again stand in two rows, as shown in the diagram, upon their almost horizontal support. It will be noticed that the flowers do not stand in the middle behind the next bract, but midway in front of another, and thus behind a third, which, however, is separated from the flower itself by that lateral one. I see only one way of explaining this strange arrangement of the flower. The branch, like the rachis, represents a distichous spike, with alternate flowers closely crowded, but is modified by the two rows of flowers having approached near together laterally, at the side of the main axis, and the margin of each bract having been interposed between the flower at its side and the bract belonging to the latter. Under this supposition we must assume the suppression of the bract belonging to the flower which stands next to the axis.

The development of this flower takes place in the following manner. The first sign of a bud, where it can be called independent, is a perfectly simple, fleshy nodule, the second stage of which is exhibited by its nearest, outer neighbour; this second bud, namely, already appears somewhat flattened at the top, and almost as if a little depressed or excavated. After this we gradually detect the parts of the flower, which however can only be recognized by their position, since they present themselves as very inconsiderable elevations. These parts are developed in the order from without inwards, in which they subsequently lie upon one another, but it is remarkable here that the stamen which is ultimately to be abortive makes its appearance before the rest, that is to say, at the same time as the inner petals, for at one epoch of the development four parts may be distinctly observed in the interior of the flower. The five other stamens do not appear until afterwards. At this epoch and for a little longer, the abortive stamen has twice or thrice the magnitude of the rest. At the outset of the development, when the various parts of the flower rise out of the formative mass, they are completely unconnected, and only begin to exhibit cohesion at the lower part when the abortive stamen has already been left considerably behind. I may observe, that it is unnecessary here to assume that originally free organs subsequently become blended together, in the true sense of the word; for, since the points of all

organs must present themselves first, while according to various observations, organs cease to grow there soonest, and the points of the petals remain permanently free, it may be supposed that the lower parts of the flower are developed in a state of cohesion. The development of stamens, where, as is well known, the anthers are complete long before the filaments begin to show themselves, offers another proof for this hypothesis. Since the two lateral outer petals are adherent to the three inner below, while, however, they must be supposed to stand in an external circle with the large, intermediate outer petal, and originate at the same epoch of development, it is natural that the two lateral outer petals should cohere only by the borders where they touch the middle inner petal, with each other and with the latter, while the borders which touch the large outer petal should remain free; which is really the case, since the border of this petal is interposed between them above,—of course, however, only towards the apex of the flower, since all are uniformly coherent below.

The only difference met with in the other species of *Heliconia* we possess here, is, that the outer lateral petals remain free somewhat lower down. In other respects all is as in *H. Bihai*. The inflorescence of these other species is the same, only the flowers are less crowded, and the outermost bract standing next the rachis is abortive, which confirms the above explanation of the inflorescence of the first-named species.

The following description of the flowers of *Musa*, as well as the diagram (Pl. V. fig. 2), show that the *Heliconiæ* differ from it not only in the inflorescence, but also in the place where the sixth stamen is suppressed. This is not indicated in the systematic works to which I have access.

Musa.

I have made out the following in the two species cultivated here. The inflorescence is simpler than in *Heliconia*, *i. e.* behind each bract (the apex of this bract sometimes grows out into a leaf) occur two transverse rows which are developed simultaneously and have no partial bracts. The three outer and three inner petals are confluent below, and the third inner, the back of which is towards the rachis, is free. The suppressed

stamen should stand here, and it makes its appearance in this place very frequently in abnormal flowers. The female flowers do not differ from the male in shape, except in the different degree of development of the sexual organs.

The very young flower of *Musa sapientum* presents itself first as a little flattened corpuscle, on which, shortly after its development, the first trace of a division is exhibited on the side next the axis, as a kind of furrow or rather a transparent line. A little later this furrow becomes deeper, and a second appears on the side next the bract, towards the top, the true apex of the bud, which furrow runs all round the latter. From the part of the flower lying outside this furrow are formed those five organs of the flower subsequently coherent together, of which the inner two petals do not become visible until after a certain interval; the inner free petal and the five stamens with the pistil are then subsequently produced from the mass surrounded by the furrow. By degrees the points are developed on the upper and outer sides of the perigonial organs, as they appear in the full-grown flower. From the central mass, as just stated, the stamens and the inner perigonial leaf appear simultaneously and form one circle. But the development of those stamens which stand before the outer petals advances much more rapidly for some time, and even in the opened flower they are still somewhat larger than the others. The pistil makes its appearance at a comparatively late period; but I could only investigate this point in what are called male flowers.

In *Musa rosacea*, which is cultivated in the botanic garden here, the development of the perigonial organs takes place in a somewhat different manner. The five segments of the flower appear simultaneously, and are uniformly developed, so that they cannot lie one upon another in the same way in the coherent flower. Moreover, the pistil here presents itself from the first trifid, just as it appears in the full-grown flower, while in *Musa sapientum* it originates simple and remains so.

Musa sapientum exhibits a multitude of interesting malformations, agreeing in this respect with most of the old cultivated plants. The following includes those which I have had the opportunity of observing:—

A. *In what are called female flowers.*

1. With 6 stamens, very frequent, the additional 6th stamen standing before the so-called labellum.
2. With 8 stamens, standing in one circle, the rest of the flower normal.
3. With 6 stamens, one, two or three of which, standing before the outer organs of the perigone, had assumed the form of the labellum.
4. With 3 labella, 8 perigonial leaves confluent, one more outside, standing behind the middle labellum, 11 stamens, 6 carpellary chambers (*frucht-fächer*), all these placed in circles around a simple pistil.
5. The labellum confluent with the rest of the perigonial organs, a free filiform body standing behind it. 6 stamens.
6. With 6 stamens, that standing behind the labellum bearing an anther.
7. With 4 perigonial leaves, all blended together, 4 stamens, 2 carpels, one of the 4 petals opposite the bract, as also one of the carpels.

B. *In the male flowers.*

1. With 6 stamens, all of normal form.
2. With 6 stamens, the 6th blended with the labellum below.
3. With 6 stamens, two of which, standing in front of the lateral, outer petals, had expanded into the form of labella.
4. With 6 stamens and 3 labella. The two additional labella standing, with a stamen, each in front of one of the outer perigonial organs.
5. The two lateral outer perigonial organs free, the lateral inner blended with the intermediate outer one. The rest of the flower normal.
6. Tetramerous flower. With 2 labella in front, then 2 free perigonial leaves right and left, and 4 others, blended together, behind. 8 stamens, one of these adherent to the pistil below, and one more added in the form of the labellum, standing in front of one of the lateral outer petals, 1 pistil and 4 carpels.
7. Twin flowers, very common, the perigone 3-parted, 2 segments in front simple, one behind 7-lobed, 5 labella, 12 sta-

mens, partly without anthers, arranged 6 and 6 round a pistil. The middle labellum interposed with a fold between the two circles of stamens, the rest of the perigonial organs forming a circle. This twin flower is also common among the female flowers.

It is seen that the commonest malformations are those in which there are transitions from one condition into another, or multiplications and confluences. Those, however, are more important in which a dimerous or tetramerous flower is substituted for a trimerous. In these, if they have petals at all, the labellum vanishes, and a stamen stands in front of each of those remaining. The flower with eight petals appears to me, like the twin-flower No. 7. B, a malformation originating through the disappearance of the organs standing at the sides where the two flowers are in contact. The labella standing side by side seem to speak in favour of this. The first of these two tetramerous flowers shows, on the contrary, that the petal next the bract is that which persists. The malformation A. 4. must be explained by a lateral doubling of the individual parts of the flower, and then the middle labellum must be regarded as an altered stamen.

Cannaceæ. *Calathea lutea*, Spr.—The flowers, as the accompanying diagram shows (Pl. V. figs. 3, 4), are enclosed in pairs in two bracts, of which the one standing on the side of the axis represents the primordial leaf (*vorblatt*)* of a shoot; these bracts, with their flowers, are again enclosed with two other flowers in two older bracts, and the entire partial inflorescence in a large dry involucral leaf (*deck-blatt*). Each individual flower possesses a small involucral leaf (*deck-blatt*) standing at its side, as looked at from the axis or from the side where the general involucral bract occurs. This arrangement of the flowers has the greatest analogy to that of the branches, except that in the latter only one branch occurs between a leaf and a primordial leaf (*vorblatt*), instead of two flowers. The unfolding of the

* The term "primordial leaf" (Bravais) or "*vorblatt*" (Schimper) is applied to the first leaf or pair of leaves of a shoot, which exhibit peculiarities; in many cases, they are regarded as representing on the shoot, the cotyledonary leaves of the primary stem.

shoots, like that of the flowers, begins at the stem side and advances towards the oldest leaf. With regard to the arrangement of the parts of the flower, it is sufficient to remark that one of the sepals stands outside, *i.e.* neither next the main axis nor the leaf, and consequently two stand where, if there were branches here instead of flowers, the axis of the branch must stand. The anther stands between these two last sepals, and on the outside of that one of these which stands beside the main axis, is observed the bract above mentioned. In this species, as well as in others with analogous inflorescence, the true bract, belonging to each branch, is suppressed in the youngest flowers, and indeed suppression of involucral bracts (*deck-blättern*) appears to be a frequent occurrence in this family generally. The primordial leaf (*vorblatt*), however, is always present. Since there can be no mistake about the import of the latter, as its position testifies to its analogy with this organ in many other Endogens, this inflorescence may be regarded as a series of successive branches apparently arising from the same point. The two flowers standing side by side are moreover to be regarded as two other branches which also arise from the same point, but whose unfolding at different times proves that they must have originally stood alternately upon their branch. The bract of each flower is suppressed, the little lateral bract appears to belong again to another absent flower, and demonstrates the branch-nature of the flower. The arrangement of the flower may therefore be explained here as distichously alternate, just as occurs frequently in nearly allied genera, such as *Thalia* and *Maranta*.

The young flower-bud first appears here as a simple gelatinous nodule, which likewise becomes somewhat excavated on its upper surface before the separate parts show themselves distinctly. The outer parts of the flower next become evident, and then the second circle, which some authors call the outer circle of the corolla. Not until both are perfectly evident, and have even assumed the leafy or scale-like form, do we see the parts surrounding the style appear, which they do simultaneously, although the anther is noticed almost first, since it is found even from nearly the beginning considerably larger than the rest of the internal floral organs. The anther stands in front of one of

the inner segments of the perigone, a little to the side, since only one of its cells is destined to be perfected; opposite to it stands the labellum, the development of which, in the very early conditions, outstrips the two lateral innermost parts of the flower. After this all remain very backward in their development, and only attain their large size in comparison with the anther, at a later epoch. With regard to the anther itself, it appears first as a little globule or vesicle, and a furrow is gradually formed on its anterior side. It deserves mention, that before the twisting and lateral development of the parts, the tooth which occurs on one side of the full-grown labellum is the oldest part of this organ, and stands in the middle of the young flower before the anther. The stigma comes to light last, as a little body excavated on its upper surface, and it rises up with the other organs of the flower. I must here again declare against any fusion of originally distinct organs; the lower parts of the floral organs do not begin to elongate until a later period, and are confluent from the first.

Two species of *Canna* which I have been able to observe in a young stage, exhibit exactly the same conditions. The petaloid filament only acquires at a late period the expansion which it exhibits in the full-grown condition, and the same is the case with the rest of the inmost organs, which in the earliest condition appear as little globules, just like the anther. The inflorescence here again agrees with the mode of ramification of the plant; the flower-branches describe a three-membered spiral round the stem; from each member of this spiral arise 2 to 3 flowers, or only 1 or 2 flowers occur with 2 to 3 bracts. The primordial leaf (*vorblatt*) we see occupy so important a place in *Calathea*, is here regularly suppressed in the little partial branches, which indicates that each 2–3 flowers correspond to a single flower, if we regard each single lateral bract of the latter as belonging to another flower.

With regard to the import of the parts of the flower of this family, the view of Lestiboudois and Lindley, according to which the more or less foliaceous organs situated inside the outer two circles of the flower are stamens, appears to me the most correct, when we take into account the history of the development. The outer two circles of the flower are quite developed at the time the

other organs make their appearance, and the latter all show themselves at once, as in the Musaceæ.

The symmetrical arrangement of the parts of a natural object, and of a plant in particular, is so general a law, striking even the uninstructed, that a deviation from it must be considered as a most extraordinary phænomenon. So far as I know, the flower of the Cannaceæ is almost the only one that can be regarded as asymmetrical. A glance at the diagram (Pl. V. fig. 5) is sufficient to prove that this flower may be regarded as perfectly symmetrical, if we assume to exist, in the midst of the two or three flowers which are found together, an axis around which the flowers are arranged in a more or less simple spiral. In this case the anther stands on the side of the hypothetical axis, just as in the Zingiberaceæ, and then consequently no distinction can actually exist between these two families. The great irregularity which we observe in the full-grown flowers arises subsequently through twisting and lateral development.

Zingiberaceæ. *Costus spicatus*, Sw.—While the flower of the Cannaceæ is difficult to define at first sight, that of the present beautiful family will be found very easy to understand. Yet after all, as I have endeavoured to show above, it is only the inflorescence which causes these difficulties. Among the proofs of this is the circumstance that the same difficulties occur in the Zingiberaceæ, if the inflorescence is not properly interpreted; only the matter is simpler here from the flowers being regular.

A glance at the diagram of *Costus* (Pl. V. fig. 6) will give an idea of the mode of arrangement of this flower and its relation to the axis and bract. Here the labellum is assumed to be a simple element, but in many Zingiberaceæ, as is well known, two little leaflets occur at its sides, which are more or less connected with it. The labellum of this species is three-lobed at the apex with very inconsiderable indentations; there is an additional smaller lobe at each side. The leaves of the species of *Costus* are, as is well known, arranged in very distinct spirals, and there also exists a twisting of the axis. The spiral of the leaves is much contracted in the spike; behind each bract stands a solitary flower with a small lateral involucral bract (*deck-blatt*), which stands in front of the flower in the direction of the prin-

cipal spiral. This small bract may be regarded, as in the Cannaceæ, as belonging to another suppressed flower, and it is consequently analogous to the two little bracts which we find at the base of the flowers in so many Dicotyledons. This frequent supposition of flowers without bracts, and involucral bracts (*deckblättern*) without flowers, would not be justifiable, were not such conditions more clearly exhibited, for example, in *Alpinia nutans* or *racemosa*. Moreover, we continually meet with one or other in the Cyperaceæ, Grasses, Bromeliaceæ, and many other plants.

The mode of composition of the spikes of a *Costus* is unusually favourable to organogenetic investigation. If we select a spike not too old, we may trace all the stages from the dehiscent fruit to the bud forming merely a milky papilla behind its bract. In this young condition I never could detect a bract at the side of the bud, but it was distinctly visible by the time the bud approached the form of a nodule. This nodule then began to exhibit an excavation in its upper surface and towards the large bract. Next, in the middle of this excavation appeared another papilla which also soon became concave; the sepals then began to separate distinctly, at least the two standing on the side next the axis. The cavity formed by the second circle of organs is at first of longish-round, but soon passes into a triangular shape. Thereupon three symmetrically arranged furrows show themselves between this excavation and the outer border of this circle, one behind each of the sides of the triangular excavation, while a little depression is observed at the place where the middle lobe of the labellum is to appear. The said furrows quickly run together and coalesce, so that soon afterwards the anther and the labellum with its three lobes are distinctly indicated. The two additional segments of the sides of the labellum make their appearance somewhat later, when the labellum, which for a short time forms with the anther a circular ridge in the interior of the flower, interrupted only by the middle lobe, separates and proceeds independently in its development. If we open a rather older flower, we find all five lobes of the labellum already developed, and the furrows of the anther also becoming evident.

The stigma deserves especial attention. It is first observed at the bottom of the flower, as a little, somewhat flattened ele-

vation, which begins very early to be somewhat emarginated above. When a little older this upper surface assumes the form of a disk inclined greatly towards the bract, exhibiting in front two distinct teeth, with a furrow below them. By degrees, that part of the stigma where the furrow is, begins to run up, more like the other side. In the full-grown condition, the teeth, which originally occupied the summit of the style, are found as a pair of little papillæ on its back, and the said furrow becomes the real stigma, in which are ultimately found the capillary cells between which the pollen-tubes make their way into the ovary.

The most interesting fact in the history of development just given, appears to me to be the formation of the anther and labellum in this flower. The anther and labellum, as we have seen, do not extricate themselves from a mass remaining in the centre of the flower, as in the other flowers observed, but a number of furrows, corresponding to the arrangement of the inmost circle, are formed in the inner side of a circle of organs already developed; not divided, it is true, but sufficiently characterized by form and position. A little later we see the anther and labellum forming one connected body, and the lobes of the latter then become apparent in this. Here therefore we might assume the production of a circle of organs by the radical deduplication of the corolline organs, which would be borne out by the development. But leaving out of the question that in *Calathea*, for instance, where the necessity of such a circle of organs exists quite as much, there is not a similar mode of development, it might equally be supposed here, that the two circles were originally confluent into one mass. And it may be urged against the first hypothesis, that at the time when the anther and labellum are still connected, the lobes of the latter are already indicated, at all events three of them, the middle one of which, alternating with the corolla, is unfavourable to this theory. But this early division of the labellum (so contrary to what is observed in other foliaceous organs) is that which, in my opinion, may on the other hand be brought to support the assumption that the original organs lying between the six outer organs of the flower and the pistil are to be regarded as stamens. Thus the course of development here is as favourable as possible

to certain speculations. To me it only tells for the present that nature here also displays the greatest variety, or that we are still ignorant of the laws which she follows here.

Orchideæ. *Epidendrum bicornutum*, Hook.—The inflorescence of the Orchideæ (Pl. V. fig. 7) is in general, as every one knows, very simple, and offers no difficulties. The curvature of the peduncle, so frequently observed, produces great variations in the external appearance of this lovely family, but it is of very slight or of no value for generic characters, although this particular is included in them by some.

In the above-named plant, very common here on rocky seashores, the bud first shows itself behind the bract as a roundish slightly flattened nodule, which is soon converted into a little cup with an undivided border, at the bottom of which the traces of the rest of the parts of the flower are seen at that time as a still undivided mass. Shortly afterwards, the outermost organs of the flower become distinct by the border of the cup growing considerably at the places corresponding to these, while no development occurs at the points corresponding to the fissures separating them. Then three little papillæ make their appearance in the middle of this flower, and directly afterwards the fourth organ, the anther, which is so situated between the lateral inner petals, that it forms a circle with them and the labellum. All these organs then increase in breadth, and the anther soon exhibits a furrow in front. The parts of the stigma appear later, at first only just indicated by a little swelling at the point of attachment of the anther. But by degrees the column rises out from the body of the flower, and the anther, which at first is quite erect, bends down upon it after its cells are perfectly developed. The labellum merits especial attention. Up to a comparatively late epoch this has so much the form of the anther, that the latter can only be distinguished from it by its greater thickness and its position. At a rather later epoch the anther is found still obtuse at its apex, while the labellum is apiculated, and at a somewhat more advanced period the labellum exhibits the processes, first the lateral notches on the border, and in particular, still later, the two *calli*, so strongly marked in the perfect flower, to which the plant owes its specific name.

Such is the course in the flower of an *Epidendrum* with the

labellum almost free, for comparison with which I have traced the development in another species where the labellum is adherent to the column as far up as the anther. This is an *Epidendrum* with almost equal sepals, the inner of which merely is a little broader, and a labellum with four *calli* on its expanded limb, which is three-lobed, the lobes being most elegantly fringed. The column with the labellum is, in the full-grown flower, about twice as long as the remaining organs of the flower. Here the young bud makes its first appearance exactly as in the above-described species, and as in the other plants spoken of, and very soon passes into the form of a cup, larger in the direction of its breadth. Inside this is first distinctly seen the labellum, and immediately afterwards the other three inner organs of the flower, in a row in front of the labellum. The rest of the development resembles that of the above-named flower, with the distinction that the foot of the column with the confluent labellum becomes elongated at a much later period. I have not been able to observe any fusion of the two organs; there is nothing blended in the full-grown flower which was not confluent at the time of its first appearance. The considerable elongation of the lower portion of the floral organs presenting itself only at a late period, may be observed, among other instances, in the sexual organs of *Cleome* and the Passifloreæ; all this must lead me to declare against a subsequent fusion of originally separate organs. In this *Epidendrum* also, the lateral lobes of the labellum, as well as the *calli* upon the surface of the limb, appear late. With regard to the column, it must be observed that the anther is not so broad in the full-grown condition as the organ upon which it rests, while in the young state it is fully three times as broad as the latter, which circumstance again indicates that mode of development of which I have spoken above.

In this *Epidendrum*, as perhaps in all *Epidendra*, the anther is found erect at a comparatively late epoch; in some *Vandeæ* I have observed this lying at the bottom of the flower at an early epoch. In *Oncidium ampliatum*, Lindley, I have seen the anther existing as a little papilla lying in the midst of the inner petals at the epoch when they first begin to expand laterally.

On the whole, the above observations of development have not

yielded me any result which can serve as evidence in interpreting the nature of the labellum and the column. The segments of the perianth generally present themselves just as they appear in the full-grown flowers, with a few exceptions which are readily explicable, and do not differ from known modes of development of foliaceous organs. That what is called an *epigynous* flower first presents itself as a simple body, as observed in all these plants, will not be found strange when we recollect that the same has long been established in gamopetalous flowers, and that in the majority of cases there is no essential distinction between flowers of the two kinds, except the radial confluence.

I may add that I am not in a position to cavil at or to undervalue observations and opinions which have emanated in part from distinguished philosophers; on the contrary, those theories are so much the more worthy of admiration, since in some cases they were necessarily set up without knowledge of the history of development. Rightly and by universal agreement have the physical sciences been ruled since the middle of the last century by direct experience, but far too much power would be claimed for this, if we condemned everything which had not yet been confirmed by it.

If now, in reviewing these four families, we direct our attention to the mode of arrangement, we are in the first place struck by the fact that the calyx and the corolla stand in an unchangeable relation to the bract and to the axis. Lindley appears to wish to make the Orchideæ an exception to this, ascribing to this family an additional outer circle of floral envelopes, occurring in *Epistephium*, of which organs one must therefore fall next the axis and two towards the bract. And he uses this as a support for his opinion of the morphological composition of the flower of the Orchideæ, to which we shall return in the sequel. Disregarding the objection that so rare a case as the appearance of a *calyculus*, even if it should occur in certain other genera, would scarcely prove anything for the entire family, unless it were accompanied by other conditions, and further, that this calyculus has not yet been investigated in its earliest conditions, &c.,—such a mode of arrangement is a very

extraordinary event among the Endogenæ and deserves little trust*. And it ought also to be noted, that in the flowers of *Musa* above described, when 3 6-parted flowers passed into 2- or 4-parted, the leaf next the bract retained its relative position. This circumstance also appears to answer the question whether the arrangement of the parts of the flower is determined by the bract or by the axis, in so far that the former keeps fixed the organ standing next above it†. On the other hand, to con-

* Through a lucky accident I have been able to settle this matter. In our lower savannahs is found a very elegant species of *Epistephium*, which I was enabled to obtain in all stages of development, at the moment when I intended to send off the above little essay. In this species the *calyculus* possesses three largish teeth standing behind the outer segments of the perianth, a small one under the labellum and a pair of indistinct little teeth, one on each side of the larger tooth next the bract. The rest of the arrangement agrees exactly with that in other Orchideæ: of other characters I have seen that the outer segments of the perianth never wholly cover the two lateral inner ones, but a thick midrib remains exposed in each of the latter. The seeds, moreover, have an appearance which seems to me unusual among the Orchideæ; the testa, namely, is expanded into a wing running round the nucleus. The development of the segments of the perianth is in agreement with the mode in which they subsequently overlie one another. At each side of the little nodule which is the first representative of the flower of this plant, we observe a little point, the first trace of the sepals, and a little later the middle sepal; at the same time with the latter, the two lateral inner segments of the perianth. Then the labellum appears, and almost simultaneously with that the anther. In this flower also the anther is at first erect, although it subsequently lies upon the summit of the column. Up to this time no trace of a calyculus is to be seen; it first presents itself clearly when the flower rises above the axil of the bract and the boundary between the ovary and the segments of the perianth becomes visible. The calyculus is persistent upon the fruit, while the other parts separate from it at a very early period. I believe I am justified in concluding from the foregoing, that the calyculus, when it presents itself in the Orchideæ, does not represent an external circle of organs, because (1) its segments do not alternate with those of that standing above it; (2) they originate later than those; and (3) because they persist upon the capsule, while the other parts become detached. I should lay much stress upon the last reason, yet I think that this calyculus must be regarded as analogous to that which may be observed on the fruits of certain Compositæ, Dipsaceæ, &c.

† In the Dicotyledons also it may frequently be observed, that the sepal which lies outside keeps its place in malformations or changes of numeral relation. Thus in the Myrtaceæ, Melastomaceæ and Onagraceæ (*Jussieua*). Several species of the last vary uncommonly in their numerical relations; one segment of the calyx always lies next the bract. The same occurs in *Osbeckia glomerata* when it presents ternary circles of organs, as sometimes though rarely occurs. How far the assumption of the position of the floral organ lying

sider the matter on all sides, the view which assumes the existence of an outer circle of organs, gives the flower of the Orchideæ a greater analogy with the Scitamineæ in reference to the relative position of the anther. Those also who regard the anther of the Cannaceæ as standing in front of a lateral inner petal, must make an exception to the rule that one of the three sepals falls next the bract standing nearest to the flower. But as it is a more logical proceeding to regard the side of the flower where the anther occurs as the real axial side, that rule may be assumed as valid here, whether that bract is present or not.

In addition to the ample number of characters which distinguish the Orchideæ from the Scitamineæ, the position of the anther, as above indicated and universally recognized, exhibits an important difference. While in the latter it stands at the axial side of the flower and embraces the style, or in certain Cannaceæ is only blended with the latter through the medium of the tube of the perianth, in the Orchideæ it stands to a certain extent upon the style and on the bracteal side. In the Musaceæ both variations of the arrangement occur simultaneously. In *Heliconia*, as above mentioned, the five stamens stand on the axial side of the branch upon which the flowers occur; in *Musa*, on the side next the bract; in *Heliconia*, moreover, the abortive stamen stands in front of the middle outer segment of the perianth. With this is combined a remarkable variation of the inflorescence, which I have already indicated above. The flowers of *Musa* standing sometimes in one, sometimes in two transverse rows, are all of one period of development, while in *Heliconia* they are developed in succession, in the order in which they approach toward the bract.

The ordinary view is, that the six stamens of Monocotyledons belong to two successive circles. Although this is very clear in theory, no proof for the assertion can be found in the course of development of the flowers here under examination. In most cases I have distinctly seen the two outer circles of organs arise in succession, but in *Musa* and *Heliconia* I have

next the axis being changeable, is applicable to the vegetable kingdom in general, I must leave to be discussed by others. In the place where I live, I must necessarily always be some years behindhand in literature, and thus it seems to me that this question has not met with all the attention it deserves.

just as distinctly seen all the stamens appear simultaneously. I have observed the same in the innermost circle of appendicular organs in the Scitamineæ, which in *Costus*, for example, appear clearly all at once*. In *Musa rosacea*, it will be recollected, even the segments of the perianth all originate at one time, so that they do not always overlie one another in the same way. In like manner we have seen the labellum of *Musa sapientum* originate with the stamens, but it would scarcely occur to any one to explain it as a metamorphosed stamen on this ground, since it is too strongly characterized by position and form, and by the fact that a stamen often stands before it in monstrous flowers. On the other hand, it cannot be denied that the said circumstance referring to the period of its development, and the frequent transformation of stamens into labelloid bodies, indicates a kind of transition from one to the other.

Few flowers indeed have been the subject of so many theories as the Orchideæ. Without enlarging upon the literature of this point, I must yet observe that Lindley, in his 'Vegetable Kingdom,' retains his older view on this subject, and only indicates an alteration on one point. While assuming, as above mentioned, an additional circle of organs on the outside, he calls the inner organs, immediately surrounding the column, metamorphosed stamens, and presumes that the stamens contained in

* In the not very distantly related Bromeliaceæ I have observed the same in *Billbergia*, although a portion of the stamens is blended with the inner segments of the perianth in the full-grown flower. Another condition allows of the conclusion of a simultaneous origin of the stamens in this flower. As is well known, the organs are all more or less twisted, and in such a manner that the petals exhibit an opposite direction to the sepals, and so on; the lobes of the stigma have the direction of the second circle. Now if the stamens originated at two successive epochs, the lobes of the stigma ought to exhibit the same direction as the sepals. The different direction of succeeding circles in twisted flowers, very evident sometimes in the calyx and corolla of the Melastomaceæ also (in the Apocyneæ where, as is well known, the segments of the calyx stand in the quincunx, the direction of the corolla is opposite to the spiral described by the sepals), is certainly most favourable to the movement of the organs in the interior of the flower during their growth. It must be remembered also that this direction, different when seen from outside, is the same where two circles touch, and that if the opposite condition occurred, the organs must be interposed between each other. How far that consideration can be used as a criterion, as I have ventured to use it in the Bromeliaceæ, I must leave for the decision of the masters of science.

the column are the inner circle of these. And then he gives up his earlier opinion as to the stigma of the Orchideæ, and assumes that its arms are opposite to the lateral organs of the outer circle of the perianthial organs.

With regard to the first point, I have already advanced some arguments against the assumption of a calyculus as typical, and cannot but think Endlicher's view, as laid down in his 'Genera Plantarum,' the more correct, chiefly because the solitary anther in every case stands in front of that outer organ of the perianth, which falls next the bract. The complicated nature of the labellum appears to me to be shown both by its so frequent confluence with the column, and by the cases where all the other organs of the perianth are blended together, and the column alone remains free. The history of development is quite silent on this point, as well as in reference to the column, at least in the above plants. But I have no doubt that the *Neottieæ* display the composition of the column most distinctly in their development, just as, moreover, the analogy of the Orchideæ with the Scitamineæ is rendered most clear by this group. In a series of monstrosities of *Ornithocephalus* in my possession, there is one which has only one simple filiform body at the bottom of the flower, and another where two such organs are observed one standing behind the other, evidently anther and column, arrested at the lowest stage of development*.

In reference to the explanation of the stigma of the Orchideæ,

* Since monstrosities in general, so interesting in many respects, do not always prove much in other directions, I cannot accord very great value to the various monstrosities observed in the Orchideæ. When three anthers occur instead of one upon a column, the additional two may just as well be called a monstrous multiplication of the central one, as a retrogression to the type; even as, for example, a pelorian *Linaria* by no means proves that the flower of *Linaria* ought to have five spurs. On this ground *peloriæ* in general ought to be divided into two groups, one comprehending those where the regularity is restored by the multiplication of an existing irregularity. To return to the Orchideæ, I have observed blossoms of *Isochilus* where in almost every case three anthers occurred instead of one; and where in one case I found only one, there were still two empty ones by its sides. But this is certainly not a further return to the type. If however, on the whole, no doubt can exist now-a-days as to the morphological import of the column, it must still be observed, that no monstrosity can demonstrate how it should properly appear, and that if ever a column should present itself separated into its elements, this might have a totally different character.

it seems to me as though the development and character of this organ might throw some light over this subject, although analogies, often only apparent, cannot wholly decide such a question. When, for instance, in agreement with their mode of development and their arrangement, we regard the two calli which occur under the stigma as the points of two carpels, the tube which leads to the germen is formed only on the outer carpel, and indeed, as it seems, on the back of it. It may be equally assumed in the Orchideæ, that the canal of the stigma is developed in that carpel falling next the bract, while the other two, lying next the labellum, may be supposed to be buried in this, which at the same time gives a kind of explanation of the frequent resemblance between the labellum and the column. Of course the many arms and branches of the latter remain unexplained here, unless we consider that this is itself a complex organ. The mode of dehiscence of the capsule of the Orchideæ favours the view which assumes six instead of three carpels in this family, and the loculicidal dehiscence is likewise analogous to that most frequent in the groups nearest allied to the Orchideæ. It is worthy of observation in the Bromeliaceæ, that in the genera which have a dry fruit, sometimes the loculicidal, sometimes the septicidal dehiscence occurs, according as the fruit is blended with the circles of organs surrounding it, or is possessed of a free superior ovary. Among the Orchideæ, the fruits of *Cryptarrhœna lanata*, R. Br.; *Dichæa graminoides*, Lindl.; and certain species of *Pleurothallis*, open on one side, *i. e.* two valves standing at the side of the column remain connected together, and the third, which stands below the labellum, separates from the others by two fissures. The ribs, which in other species separate from the placentiferous valves, are entirely wanting here. It would seem as if the firmer combination of the valves below the column, in these cases, was produced by the stamen occurring above them. But it must not be forgotten that in all these cases the septa, or in one-celled fruits the placentas, alternate with the sepals.

The mode, however, in which a fruit bursts, cannot prove anything concerning its morphological nature. The great variation which prevails in this phænomenon, the circumstance that otherwise very nearly allied genera exhibit essential differences

in this particular, testify that no great stress can be laid upon this part of vegetable life, in regard to the import of organs. In this case, as in all others, an earnest study of the arrangement of the organs will, sooner or later, probably solve the question.

DESCRIPTION OF PLATE V.

Fig. 1. Diagram of *Heliconia*. B, Universal bract; *b*, partial bracts,—the figures show the flowers to which these belong. *Ax*, main axis; *ax*, axis of the branch. The noughts (O) indicate in this, as in the succeeding diagrams, the places where stamens are abortive; the points (·) actually existing stamens or anthers. Where a nought is crossed through (Θ), it indicates a petal taking the place of a stamen.

Fig. 2. Diagram of *Musa*.

Fig. 3. Diagram of *Calathea*, showing how the flowers are enclosed in a bract and a floral leaf (*vorblatt*); *b b*, little bracts.

Fig. 4. Diagram of a single flower of *Calathea*.

Fig. 5. Diagram of *Canna*. 1B, 2B, 3B, large bracts; *b* and *c*, small bracts.

Fig. 6. Diagram of *Costus*. B, large bract; *b*, lateral, small bracteal leaf (*deck-blatt*).

Fig. 7. Diagram of *Orchideæ*.

[A. H.]

Article VII.

Fragments relating to Philosophical Zoology. Selected from the Works of K. E. von Baer.

[THE translator feels some apology necessary for the present departure from the principle which ordinarily guides the Editors of the Scientific Memoirs;—the principle, that is, of reproducing the work translated in its entirety and completeness.

There were two objections to pursuing this course with von Bär's writings. In the first place they are voluminous, and in the second, they are between twenty and thirty years old; so that they would have required notes and corrections as voluminous as themselves to bring them, in matters of detail, up to a level with the present state of our zoological knowledge.

On the other hand it seemed a pity that works which embody the deepest and soundest philosophy of zoology, and indeed of biology generally, which has yet been given to the world, should be longer unknown in this country*. The present selections have therefore been made, and it is hoped that they embody all the important points of von Bär's doctrines. The translator will be more than gratified, if yet, during the lifetime of the venerable author, he should be the means of assisting to place in its proper position the reputation of one who had in the completest manner demonstrated the truth of the doctrine of Epigenesis three years before the delivery of Cuvier's *Leçons sur l'Histoire des Sciences Naturelles* (in which he still advocates the Evolution theory); and who had long recognized development as the sole basis of zoological classification, while in France Cuvier and Geoffroy St. Hilaire were embittering one another's lives with endless mere anatomical discussions and replications, and while in Germany the cautious study of nature was given up for the spinning of *Natur-Philosophies* and other hypothetical cobwebs.]

* Dr. Carpenter (Principles of General Physiology) is, so far as we know, the only English physiologist who has publicly drawn attention to Von Bär's philosophical writings.

I. *The Relations of Affinity among the Lower Forms of Animals.*

[From the *Beiträge zur Kenntniss der niedern Thiere, von* K. E. VON BAER, *Nova Acta Physico Medica*, 1826, t. xiii.]

From the time when the author of these essays first began to occupy himself seriously with the study of the animal world, he thought he could observe that the ordinary conception of the mutual relations of animal forms was not true to nature, and peculiar views concerning the so-called affinities of animals arose in his mind. So far back as the year 1819, he began to print these views, but ceased his attempt when he had reached the fourth sheet, partly because the development of these principles led him further than he had expected, partly because he desired to make further personal investigations. Since that period, however, his conception of the mutual relations of animal forms, remaining fundamentally unchanged, has more and more perfected itself. This is not the place, nor is there sufficient room here to demonstrate it completely, for the proving of the principle appears to him to be at present the chief matter, which is impossible without entering into the essential peculiarities of animal structure and their relations to the rest of nature, by which they are conditioned and rendered intelligible. However, the results of the preceding investigations have led him to relations of affinity whose truth will not be granted so long as another system of animals is regarded as perfectly natural and true. Hence, as a corner-stone to the preceding treatises, it seems advisable to attempt a clearing up of the so-called affinities of animals.—(p. 731, 732.)

If we take any one of the principal forms of invertebrate animals, we find it in many stages of development, and descending in a more or less uninterrupted series down to the Protozoa. Even the vital characteristics which are manifested in the higher grades, are indicated in their first commencement. The elongated *Vibriones*, the prototypes of the Naidæ and Nematoid Worms, and with these of the Insects, are distinguished by their swift and uninterrupted movements beyond all other Infusoria. We must, however, take care not to confound the *Bacillariæ*, which to us appear to be true plants, with the *Vibriones*. The *Paramœcia*, prototypes of the Trematoda, shorter and broader

than the *Vibriones*, are less active, but very much surpass in this respect the globular *Volvoces* with their allies. The lower animals teach us, what we have already learnt from the chaotic dwellers in the Mussels, that the kind of movement (which is here almost the only manifestation of life) depends upon the form of the body; thence a duplex movement where the body, as in the *Cercariæ*, is composed of two forms. On this account indeed, Müller's characters for the genera of the Infusoria, which are taken, not from the general figure of the body, but from non-essential organs, hairs and spines, are so little fitted to yield natural groups, and leave us in want of an altogether new nomenclature, and of new definitions of the genera.

In order to obtain a just insight into the mutual affinities of animals, it is before all things necessary to distinguish the different *types of organization* from the different *grades of development*. The general neglect of this distinction seems to us to have led to the strangest approximations. We have the Cephalopods supposed to form a transition to Fishes, and the Echinoderms connecting Polypes with Intestinal Worms. But metamorphose a Cephalopod as you will, there is no making a fish out of it, save by building up all the parts afresh. Granting that the Cephalopods are the most developed Mollusks, and that the Fishes are the least developed Vertebrata; and that therefore there is a certain approximation between them, so far as regards the degree of development; yet to the unprejudiced eye they present no closer affinity, *i. e.* agreement in formation. Can it be denied that a Pike is infinitely more similar to Man than a Sepia? As little can we recognise any affinity between the Starfish and the Tapeworm. In the former the repetition of structure is successive in a circle, in the latter in a longitudinal direction. That is the sole agreement. But even in this there lies a contrast.

Our persuasion, that the grades of development must be distinguished from the types of organization, is founded upon the following considerations:—We know that all the functions of the perfect animal body contribute to a general result,—to the life of the animal; but also that the general mass manifests the total life (for animal life is always a totality); that the albuminous jelly of the Polype digests, breathes, contracts, feels, and propagates; that, however, all these functions go on as it were in

common, or but slightly isolated, just as the whole mass of the body is a homogeneous mass. With a greater separation and more complete independence of these functions is combined a greater differentiation of the body into organic systems, and of these systems again into separate more individualized sections. In this consists the higher development of the animal body.

But the mode in which these organs of the animal body are united together, is a wholly distinct matter. And it is to this manner in which the organic elements are combined that we give the name of *Type*. Every type may be manifested in higher and lower degrees of organization; the type and the grade of development together determine the special forms. Therefore for every type there exist grades of development which here and there form considerable series indeed, yet which are in no uninterrupted succession of development, and are never equal through all grades.

Although then, in the following pages we speak of certain series of grades of development, we are far from wishing to assert any equal distribution of forms through these. On the other hand, we think it obvious that the assumption of any such corresponding affinities among organic forms does violence to nature. Whatever such scheme may have been devised, it cannot be discovered by the unprejudiced observer. If such a correspondence be deduced *à priori* from the harmonious operation of nature, we may demonstrate with equal justice and force that among men A must have as many relations as B, because such equivalency of relationship is contained in the idea (*denkbar*), and therefore must be; and that if B even gave out he had fewer brothers, they would nevertheless be discovered some day or other. It appears to us that here the necessarily regular occurrence of the phænomena has been confounded with their mutual equivalency. For instance, to resume the comparison which the word *affinity* has suggested: as the small number of children in a family is not a matter of chance, but depends upon the slight fecundity of the parents; so it is no chance or whim of nature that certain animal forms are realized in fewer variations, and exhibit fewer deviations than others. The reason must lie in the nature of these forms. Certain combinations of organic parts are, to speak metaphorically, more natural than others. A

bird's beak must be more in harmony with a bird's body and more easily combined with it, than with a mammalian body, and still less with a frog's body; for with a multitude of beaked birds, we have only a couple of beaked mammalia, and no beaked frog at all. Here we have, not to interpret, but to conceive what actually exists.

We see in fact, that certain principal models of the animal kingdom become modified among various animals, not however equally, but in such a manner that the majority of these modifications are more closely allied than the rest. The principal models may be called Provinces of the animal kingdom, and their most important modifications, Classes; these being again modified into subordinate forms, Families, and so forth. It happens always, however, that among the subordinate modifications of any degree, the majority resemble one another, and only a few diverge; so that the organic theme with its variations may be compared to a sphere composed of a densely compressed centre and a much more thinly populated atmosphere. Upon the same relations again depend what we call *genus* and *species*. The species consists of a number of individuals, which are indeed not perfectly similar, but most of which exhibit an obvious similarity; whilst a few are often so aberrant, that it might be seriously doubted whether they are to be grouped under this form or not. These aberrations, however, are not only rare, but Nature affords them less support, so that they continually tend, either in themselves or in their progeny, to return to the normal standard. There are, further, two remarkable laws: the first, that the more dense the centre, the less extensive is the atmosphere, as well in the larger spheres as in the smaller subordinate ones. So even in the species. If the individuals which may be unquestionably referred to one species, yet differ a good deal from one another, then the number of those concerning which well-founded doubts may be entertained, is not inconsiderable. The more similar, on the other hand, the normal individuals are to one another, so much the less frequently, or even not at all, do the transitional forms occur. Secondly, in every larger sphere the subordinate spheres of the centre are richer in secondary forms than the sphere of the periphery. In fact, if we take single species, we find that they are the more rich in indi-

viduals, and the more extensively scattered over the earth's surface, the more closely they are connected with the centre of a sphere of modification.

What has been said may be made more intelligible by examples. I choose them from among the Vertebrata, and, indeed, from the higher classes, because our acquaintance with these is least defective. The Mammalia differ so much from one another, that without anatomical examination they could hardly be recognised as modifications of one principal form. Their centre is evidently formed by the proper quadrupeds, while the climbers (Quadrumana), the fliers (Cheiroptera), the swimmers (Cetacea), and lastly the Monotremata, represent the atmosphere, or the aberrant forms. The proper quadrupeds even present considerable differences from one another; still more do the peripheral forms differ from one another and from the central forms. They considerably approach other principal forms, without however truly passing into them; for the organization of the most aberrant forms, the Ornithorhynchus and the Whale, is still so far removed from that of a true fish or amphibian, that we can decide with certainty to which class they belong. It is otherwise with Birds. All the orders are so similar in their essential relations, that we find them as it were crowded round the centre, and only the Ostrich with a few other birds can be regarded as the peripheral members of this very condensed sphere. These peripheral members again do not deviate so far from the principal forms, but that the hastiest inspection is sufficient to leave no doubt on the mind, whether they are beasts or birds. Enclosed within these narrow bounds, the number of Birds is yet at least six times as great as that of the Mammalia. The peripheral forms among Birds are to the central forms, hardly in the proportion of 1 to 1000: in the Mammalia they form more than one-fourth (!) of the whole. If we turn to the subordinate spheres, we find in the centre of the Mammalia a few families whose normal genera are very similar to one another, as the Ruminants. Here the number of the peripheral forms (the hornless Ruminants) is not only small, but they are likewise few and scattered in the world (Camels are multiplied only by human aid), in comparison with the herds of Antelopes, Deer, and Oxen. The Carnivora, whose centre is

formed by the Cats, Hyenas, Dogs, Viverridæ, and Weasels, are much more unlike one another, and so form a less consolidated sphere than the Ruminants. So much the more numerous and more nearly approximated to other families are their transitional forms, by which in the Potto they approach the Quadrumana; in the Insectivora, the Rodents; in the Fish—the Otter, the Seal and the Walrus, the Cetacea; in the Marsupialia, the Monotremata; and these transitional forms are upon the whole far poorer in individuals than the aberrant forms of more narrowly limited families. The Rodents present nearly the same peculiarities. Among the proper quadrupeds the least consolidated sphere is that of the Pachydermata, which, however, in relation to the small number of those forms which can be considered central, has many aberrant members,—the Daman, the Elephant, the Solidungulata; and in the ancient world there were yet more. Among Birds the transitional forms are more solitary genera,—the Ostriches and Cassowaries, which under the influence of the more consolidated centre are only single mutually divergent groups. Among the Mammalia, where even the central forms are not so closely arranged, the transitional or atmospheric groups themselves compose considerable spheres. The Quadrumana, a transition to Man, form a numerous order, whose centre is constituted by the true Apes; while the Makis, the transition to the proper quadrupeds, form single small scattered families. Not so the Bats, for which the genera *Pteropus*, and still more *Galeopithecus*, are transitional forms. Most distant from the centre of the proper quadrupeds are the Monotremata; and in accordance with this we find that they contain but few genera, among which considerable differences exist, and that even the species are represented by but few individuals. If we glance at the Amphibia, we find that the members of the most aberrant group, the Sirenidæ, are not only more dissimilar from one another, than, for example, all the tail-less Batrachia which occupy the centre are, but that their occurrence is limited to a few places.

Do not these considerations show that the Idea of animal organization does not vary at equal intervals, but, as we observed above, is realized in certain principal forms which again break up into variations of a lower grade, in such a manner that the

variations are more or less closely accumulated around a given centre, according to the peculiar nature of each standard form? It follows at once, from this that the transitions are more indicated than realized, that they are very unequally distributed, and that they never form an even progression; for at the limits of two spheres, the most similar members of each are far more remote from one another than they are from their own centres?

The conception of spheres does not exclude that of series; on the other hand, the different types, since a manifold degree of development occurs in them, will necessarily arrange themselves in series, which however again consist of spheres, radiating from whose centres every single form varies in many directions.

Four principal types appear distinctly to manifest themselves; the type of the elongated, Articulated animal, the type of the Radiate animal, the type of the Mollusk, and that of the Vertebrate animal; the latter unite the articulate and molluscous type together in their animal and vegetative organs. Indeed one might perhaps recognise in the head an outline of the radiate type, since here in the course of further development all parts become more and more collected around a central point. Besides this, in any case the central portion of their nervous system is something peculiar which is wanting in other animals; for which reason the Vertebrata cannot descend to the lowest grades of organization.

It will be seen that we have here arrived at the four principal divisions of the animal kingdom established by Cuvier. We believe, in fact, that Cuvier has penetrated most deeply into the relations of animal organisms. But he does not satisfy us in this; that he requires in the Mollusca and Articulata not only the type of their organization, but also a certain degree of development,—a condition which can only be required of the single classes. The consequence is, that all the animals of low organization are thrown among the Radiata, although very many of them are by no means radiate in their structure. The boundaries under these circumstances could only be drawn arbitrarily. If *Gordius* belongs to the Articulata, why should not *Filaria* and *Vibrio*? It seems plain to us that the conditions which predominate in this type may be traced down to the lowest stages of organization; only we must not require from these prototypes,

that the special details of the parts, *i. e.* of the intestinal or nervous systems, resemble what is found in the higher grades; for the intestine and the nervous system themselves are not always present; it needs only that the general character should be recognised. We thus obtain principal series between which again subordinate ones are found, according as in them the character of one type is more or less mixed up with that of another. These series again send out offshoots, and by no means always take a rigidly straight course, since every series is fundamentally only a number of spheres. After what has been said, it will cause no astonishment if we neither make the series equally perfect, nor draw them out to an equal length. It seems to us rather, that there is evident reason why gaps must exist here and there (pp. 738–747).

What do we gain, however, by this view of the lower forms of animals? We ask in the name of the reader. We gain, I believe, a great deal.

In the first place we safely base the conviction, that all the forms of animals are by no means to be considered as uniserial developments from the lowest to the highest grade of perfection. Although from the Vibrio to the Butterfly intermediate forms occur, though not at equal intervals, nor of equal development, which manifest in their form and life the grades of a common character,—yet no starfish nor shellfish can be intruded without completely destroying the fundamental conception of a genetic connexion. The same relations are repeated in many fundamental types. In order to show at once the application of our views to special investigations, we must call to mind that the metamorphoses of animals in time have been compared with the stages of development considered as isolated, or the so-called metamorphosis in space. It has been concluded by a bold generalization from a few analogies, that the higher animals run in the course of their development through the lower animal grades, and sometimes tacitly and sometimes expressly they have been supposed to take their way through all forms. We hold this to be not only untrue, but also impossible. The general type appears to us to be always unchanged, and we observe that animals in the course of their development are more or less similar only to lower stages of the same type. The insect may per-

haps resemble a Vibrio or a Thread-worm; but never a Medusa or an Ascidian. In the Vertebrata, indeed, it has been attempted to demonstrate an agreement with Medusæ—in the distribution of the vessels in the germinal membrane! Here the *only* thing overlooked was the body of the embryo. In this the essential character of the type is the first to arise; the formation of the vertebrate animal begins with the rudiment of the vertebral column, proceeding from which the dorsal folds pass upwards and the visceral plates downwards, so as to lay the foundations of the upper and lower halves of the body, which characterize this form.

Our view explains also, how the external forms of animal bodies are connected with their vital manifestations, and with the arrangement of the internal parts. The separate organic elements develope themselves into a higher state of perfection by differentiation of the animal substance. Their form and connexion, however, depend upon the type which predominates in the animal, or in a principal part of it. Hence from the form of the exterior one can conclude the arrangement of the interior. If we examine, for instance, an Octopus, we see the molluscous structure only in the sac-like part of the body, while in the head the motor organs are arranged in a completely radiate manner around a central point. In the middle is the aperture of the mouth, and it corresponds completely with the type of the radiate animal, that the nerves and vessels, before they pass into the separate arms, are combined into a circle in the median disc. We know again that the Cephalopoda most frequently swim with their heads directed downwards; the radiate portion of the body therefore seems to hold and to move itself in accordance with the mode of locomotion prevalent in its type, overcoming the tendency of the molluscous body. Even in the higher animals we find that when single parts take on the external form of the radiate type, we have a corresponding order of the nerves and vessels. Thus it is with the iris of the Vertebrata.

Furthermore, our conception explains how, according to the nature of the different types, a given organ arises, and becomes developed earlier in one than in another; how it is again that the perfection of a single organ does not imply a general correspondence in development. It is one of the characters of our

first type that the principal vascular trunks are tubes, and a true sharply defined heart appears only very late in the already modified form of the Decapoda. In the radiate type we have rings united by a perpendicular vessel. In the molluscous type, in which there is a general tendency to the formation of vesicles, the central point of the organization naturally appears earliest as a distinct heart. The French zoologists then are greatly in error in regarding the Mollusca from this organ alone as more highly developed than the Insects, and in placing the Acephala above the Bees.

Finally, this idea enables us to comprehend how the general form of the type depends upon the productive conditions (*zeugenden momenten*), while the inner development depends especially upon the nature of the animal.* Perhaps these considerations may be profitable if they be kept in view in the course of investigations into the course of development.

II. *On the Development of Animals, with Observations and Reflections.* By Dr. K. E. VON BAER, Konigsberg, 1828.

[*Ueber Entwickelungs-Geschichte der Thiere, von* Dr. K. E. VON BAER. 4to, 1828.]

THE FIFTH SCHOLIUM.—On the relations of the forms which the individual takes in the different stages of its development, pp. 199–264.

§ 1. *The prevalent notion, that the embryo of higher animals passes through the permanent forms of the lower animals.*

The relation of the forms which the embryo gradually assumes has already been referred to in its proper place in the course of the exposition of the mode of development of the chick. The importance of the subject, however, and the interest with which it has lately been regarded, lead me to think it fitting and necessary to undertake a special investigation of these relations, since they appear to me to be somewhat different from what the general opinion represents them. In order to be clearly understood in developing my own views, and to bring forward more distinctly their essential features, I must be permitted first to explain the prevalent mode of conceiving the progress of the development of the embryo.

Few expressions of the relations of organized beings have met

with so much applause as this:—*that the higher forms of animals in the single stages of the development of the individual, from its first origin to its completed development, answer to the permanent forms of the animal series, and that the development of each animal follows the same laws as that of the whole animal series; that therefore the more highly organized animal in its individual development passes essentially through the permanent forms which lie below it, so that the periodical differences of the individual may be referred to the differences of the permanent animal forms.*

This idea, springing into existence at a time when no connected investigation (except those of Malpighi and Wolff) into the earlier periods of development of any animal had been instituted, and principally carried out by a man who perhaps possessed more knowledge than any one else of the course of development of the higher organisms, could not fail to be widely accepted, since it was supported by a multitude of special demonstrations. It acquired yet greater influence, by its fruitful application to the explanation of a series of monstrosities, which were regarded as the consequences of a partial arrest of development in its earlier periods. It is no wonder then that it was warmly received and rigorously carried out.

Certain of its advocates were so zealous, that they no longer spoke of similarity, but of perfect identity, and assumed that the correspondence had been demonstrated in all cases and to the minutest details. A short time since we read in a paper upon the circulation in the embryo, that there was no animal form through which the embryo of man omitted to pass. By degrees it became the custom to look upon the different forms of animals as developed out of one another, and then many appeared to forget that this metamorphosis was after all only a mode of conceiving the facts. On the strength of the observation that no vertebral remains are to be found in the older strata, it was concluded that there was historical evidence for such a metamorphosis of the different forms of animals, and at length, in sober seriousness, and with all due particularity, we were informed exactly how they arose from one another. Nothing could be easier. A fish, swimming towards the shore, desires to take a walk, but finds his fins useless. They diminish in breadth for want of use, and at the same time elongate. This goes on with

children and grandchildren for a few myriads of years, and at last who can be astonished that the fins become feet? It is still more natural that the fish in the meadow, finding no water, should gape after air, thereby, in a like period of time, developing lungs; the only difficulty being that in the meanwhile a few generations must manage to do without breathing at all. The long neck of the heron arose from a habit its ancestors acquired of stretching out their necks for the purpose of catching fish. The young ones in consequence came into the world with their necks something the longer, and cultivated the same trick, transmitting to their posterity still longer necks, whence we may fairly expect, that when the world is getting very old, the herons' necks will be past measuring altogether.

An immediate consequence of the assumption of this idea as a natural law was, that a view which had once been very general, but had subsequently been pretty generally given up—that of the universal progression of the different forms of animals—gradually got footing again; and though not often asserted in so many words, nay, perhaps unconsciously to naturalists themselves, it became admitted in discussions concerning animal forms. It must be confessed that the natural law being assumed, logical consequence required the admission of the view in question. There was then only one road of metamorphosis, that of further development, either attained in one individual (*individual metamorphosis*). or through the different animal forms (*the metamorphosis of the animal kingdom*); and disease was to be considered as a retrogressive metamorphosis, because universal metamorphosis, like a railroad, allows motion backwards or forwards, but not to one side.

From such applications, opposed at once to unprejudiced investigation and to exact knowledge, the more cautious indeed, and before all that advocate of the principle through whose name it attained the widest assent, carefully abstained; but it cannot be denied that they were the logical consequences of the law, and thence a sufficient ground of distrust*. But the attacks of

* It did not appear fitting here to give a detailed account of this theory, for the purpose of attempting to refute it. Since a certain contradiction appeared perceptible enough in Nature, it has been carried out by different men very differently. Those who were best provided with special knowledge were

its adversaries were partly directed only against the exaggerations, partly were weak in not being supported by careful personal observation of the development of the same animal form.

A few exceptional cases can have but little weight, unless a completely new doctrine can be substituted. The gradual development of the embryo out of a delicate homogeneous mass, called to mind so strongly the construction of the body of the lowest animals, that all objections appeared wasted against unimportant minutiæ, so long as the attempt was not made, recognizing this agreement, to demonstrate another and a different relation.

Quite recently, in fine, the doctrine of the agreement of individual metamorphosis with the ideal metamorphosis of the whole animal kingdom obtained an additional importance, by Rathke's brilliant discovery of gill-clefts in the embryos of Mammals and Birds, in which very soon afterwards the appropriate vessels were found.

always more cautious and indefinite, while those who followed them were much more decided. The whole doctrine appears to me to be more a phase of the development of natural science than the property of any single man. Different degrees of development were observed in the different forms of animals. It was recognized that these animal forms are to be considered as modifications of one another. It was natural, in fact necessary, that the attempt should be made to carry out the simplest mode of conceiving these modifications, that all forms are immediately developed out of one. The assumption of this development as an historical fact, can be considered but a small step further, and is a logical deduction; a comparison with individual development came necessarily into the same circle of ideas; and in any case it is a service to have made the experiment how far our knowledge of development can be introduced therein.

With the full conviction that the view in its whole extent is a necessary transitional phase of our knowledge of nature, it seemed unnecessary to the short exposition given above, to follow an exact chronological order. Many of the attempts indicated, to show the development of the classes of animals one out of the other, are older than the more important endeavours to refer the stages of development of the embryo to the class-differences. All this I know very well, and I expect no objections on this head. I chose only the shortest mode of exposition. The whole circle of ideas, which I here hope to define more exactly, by drawing attention to the distinction between the higher and lower stages of development of the animal body and the type of organization, has so large a share in all investigations, that we meet with it in a very great number of works, and it is therefore quite unimportant to make a selection here.

§ 2. *Doubts and Objections.*

At an early period my attention was directed to the mutual relation of the permanent forms of animals; and the first thing that appeared obvious to me was, that this relation could in nowise be considered as a uniserial progressive development. But a uniserial progressive development, if only as a logical conception, appears to be absolutely necessary for the permanent forms of animals, if they are repeated in the development of the individual.

I therefore regarded this doctrine with mistrust, and kept it constantly in mind in investigating the development of the chick, in the persuasion that the continued observation of the development of a single species of animal must yield a more certain decision than a multitude of single unconnected comparisons. As, however, my observations convinced me that the essential character of the vertebrate animal arises very early in the chick, and regulates the whole course of its development, I so early as the year 1823 expressed my doubts in the form of an academical disquisition*. Nevertheless it seemed fitting not to speak publicly concerning them until I could present a series of observations. My conviction with regard to that law, indeed, was more a negative one. I now believe that I can replace it by another; and the first part of this collection offers, I think, a proper opportunity for the development of the latter.

It will not be superfluous first of all to bring forward a few objections to the view just alluded to, which might be drawn from the previous investigations of embryos, and which might serve to raise doubts in the minds of those readers who are completely devoted to it. Not attempting a complete development of these doubts, I shall content myself with a few brief indications.

In the first place, I was led to reflect, that we know the development of hardly any but the highest forms, the development of Mammalia (including Man) and that of Birds. In whatever

* Dissertatio de fossilibus Mammalium reliquiis. Regiomont. 1823, 4to. To which is appended the thesis, *Legem a naturæ scrutatoribus proclamatam, evolutionem quam prima ætate quodque subit animal quam in animalium serie observandam putant, respondere, a natura alienum esse contendo.*

circumstance their embryonic condition, therefore, differs from their permanent state, if it had an analogue anywhere in the animal series, it must be found almost always among the lower animals.

That, however, a few correspondences should be found between the embryonic condition of certain animals and the perfect condition of others appears to be necessary, and of no particular importance. They could not be wanting, since the embryos do not lie without the sphere of the animal world, and since the variations of which the animal body is capable are determined for each form by an internal connexion and mutual reaction of its separate organs, whence certain repetitions become necessary.

To convince oneself that such a doubt is not wholly without its weight, let it be imagined that Birds had studied development, and that it was they who in turn investigated the structure of the adult Mammal and of Man. Should we not find something of this sort in their physiological handbooks? "Those four-legged and two-legged animals have much resemblance to embryonic forms, for their cranial bones are separated, and they have no beak, just like us during the first five or six days of incubation: their extremities are a good deal alike, as ours are for about the same period; there is not a single true feather over their whole body, but only delicate feather-shafts, so that we, as fledgelings, are more advanced than ever they are; their bones are hardly at all brittle, and like ours during youth contain no air at all; they have no trace of air-sacs, and their lungs are not adherent, like ours at the earliest period; they have no crop; their proventiculus and gizzard are more or less compounded into a single sac; evidently arrangements which in us are only transitory, and the nails are in most of them as clumsily broad as in us before we break the shell; the Bats alone—seemingly the most perfect among them—have any power of flight, which is quite absent in the rest. And these Mammals, which for so long a period after birth cannot find their own food, and which are unable to raise themselves from the earth, must pretend forsooth that they are more highly organized than we!"

If it be a law of nature that the development of the individual *essentially consists* in passing through the permanent forms of lower animals, it must follow—

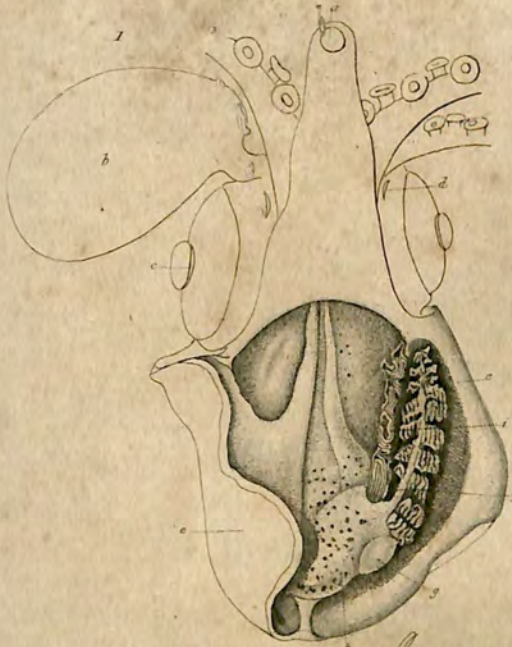
1. That no conditions can obtain in embryos which are not permanent in at least some animals. There exists, however, no animal which carries about its nutriment with it, as the embryo carries its yelk. No animal has a protruded portion of the intestine, such as the yelk-sac. But from the development of Birds, and of some Mammalia (especially of the Carnivora), in which this yelk-sac remains for a very long period, up to a time when all the characters of the Bird's or Mammal's body are either fully present or nearly so, we ought to conclude that many such animals exist. Among Mammals the incisor teeth are developed before any others. No animal, however, has a permanent dentition consisting of incisor teeth only.

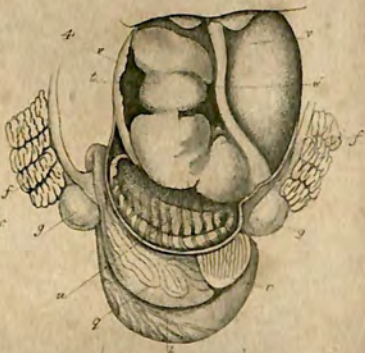
2. In like manner, however, as the relations of the embryo produce forms in it like the protruded intestinal sac, which occur in no permanent animal, do they render it impossible that many large groups of animals should be repeated. Thus the essential characters of Insects, their active relation to air, cannot be repeated in them; therefore, also, the Mammalian embryo can never resemble the perfect Bird.

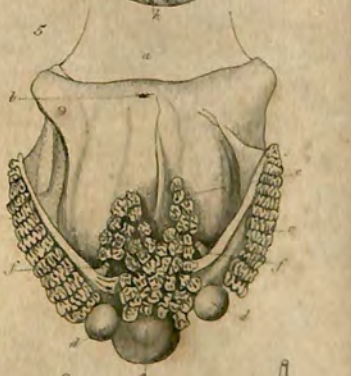
3. Furthermore, the embryo of the higher animals, in any stage of its development, should not agree with a *single* character only of some permanent form, but with its totality, even although the peculiar relations of the embryo should exclude certain correspondences. If it be argued, for instance, that certain characters must be peculiar to, and permanent in, the embryo as such; that, for example, it is only because as an embryo it is dependent for nourishment upon the maternal body, that it has a protruded yelk-sac, and in this respect cannot correspond with a permanent form; yet those relations in which there is an agreement here and there* must be common to all. This, however, is not the case. If I ascribe to the embryo, so long as its two cardiac ventricles are not yet separated, and the fingers are not divided from one another, the organization of a Fish, yet I find no compressed tail, nor a thousand other characteristics which very early appear in Fishes.

It is just the same with whatever permanent animal form I compare the embryo of a higher form. It is said that the Cetacea are fœtus-like (*i. e.* resemble the embryos of higher animal

* *i. e.* which are not necessarily connected with embryonic existence?—Tr.







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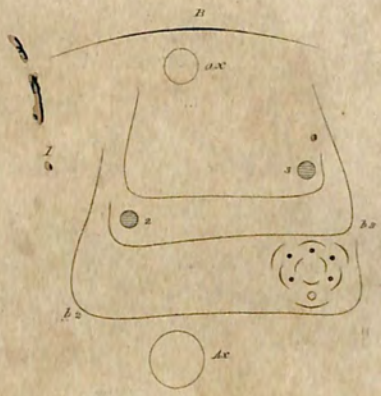
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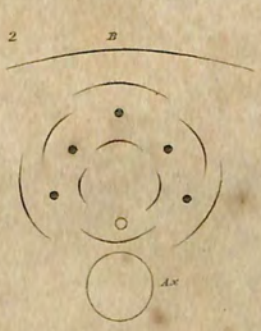
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forms), because their testes are contained in the abdomen, because some of them have no true teeth, because the anterior and posterior sphenoids remain separated, &c. &c. But the other cranial bones of the Cetacea unite very early and very closely, and therefore are adult-like. Their jaws are very long, although all Mammalia, the Cetacea included, have their jaws the shorter the younger they are. The separation of the cranial bones, however, is no especial peculiarity of the embryonic condition, which is absent in the adult condition of the lower classes of animals; for in Fishes it is brought forward again as an embryonal condition that the cranial bones are divided into many portions, and are merely applied to one another, although at the base of the skull the unity of the sphenoid—the very opposite of what occurs in the Cetacea—offers, on the other hand, a resemblance with the adult condition of the highest Mammalia. Agreement with a Fish or with a Cetacean is therefore no absolute condition for the organization of the embryo.

4. If the law we are engaged in investigating were correct, no conditions which are permanent only in the higher animals could be a transitory stage in the development of particular lower forms. But a great number of such conditions are demonstrable. We cannot indeed discover them in the course of human development, since we know no higher organization. But the Mammalia afford examples enough. In all the jaws are at first as short, as they are permanently in Man; the parietal ridge is developed very late in animals which are provided with it, while, on the other hand, it is wanting in the highest forms. Instances of this kind multiply the further we descend. We have already introduced Birds speaking, in order to insist upon a multitude of previously-known relations in which the embryo of the Bird agrees with the adult Mammal. We can bring forward still more. The brain of Birds in the earliest third of embryonic life is much more similar to the brain of Mammals than in the adult condition. The corpora quadrigemina have not descended, the olfactory bulb is hollow and thick, and there is even a kind of fornix present. The heel of the Bird developes itself from many cartilages into a single bone. The eyes in the Chick are at first placed nearer together than subsequently, and give it a humanized face. Young Lizards have a very large

brain. The larva of the Frog has a true beak like Birds, and before it loses its tail an intestine of a length such as is only to be found permanently in a few forms of Mammals. The Frog larva is at first tail-less, a condition that occurs only among the highest Mammals; even the adult Frog has an internal tail, for we must so designate its long caudal vertebra. The Myriapods, the Mites, and the Hydrachne have, when they creep out of the egg, only three pair of feet, like the perfect condition of Insects which undergo metamorphosis. Even if, contrary to my opinion, it be maintained that the Arachnida are more highly developed than the true Insects, yet every one will allow that Insects with a metamorphosis are higher developments of the Myriapoda. Such cases as these should by no means occur, if the development of the higher animals consisted in passing through the forms of the lower ones.

5. We ought to see the organs or larger apparatuses make their appearance in the different classes of animals in the same manner as they are developed in the embryos of higher animals, if we consider the former to be developed out of one another; this, however, is by no means the case; the posterior extremity is in most Fishes only perfect in its terminal member, while in the embryo of the higher animals the proximal joint is first formed.

6. Lastly, such parts as are found only in the higher animals should arise very late in the course of development. But it is not so. A few portions of the vertebral column, its centre and arches, exist earlier in the Chick than every other part. How then can the Chick ever have any similarity with an invertebrate animal?

This remark, however, leads us nearer to our purpose, and therefore at this point the attempt to discover the true relation may be made.

§ 3. *On the Mutual Relations of the different permanent Forms of Animals.*

In order to investigate the essential relations of the metamorphoses which occur in the development of the individual, I must premise a sketch of the different forms of animals. I have already in part treated of this subject in another place (*Nova Acta Acad.* vol. xiii. part ii. pp. 739–762); but since the re-

marks which I have there made find their application here, and since besides it is accessible to but few, I shall not hesitate to prefix an extract from that essay for the purpose of building further upon it.

I wish before all things to draw attention to the distinction between the *grade of development* of an animal and the *type of its organization.* The grade of development of an animal consists in the greater or less heterogeneity of its elementary parts and of the separate divisions of a complex apparatus; in a word, in its greater histological and morphological differentiation. The more homogeneous the whole mass of the body is, so much the lower is the grade of its development. The grade is higher when nerves and muscles, blood and cell-substance, are sharply distinguished. The more the elementary parts differ from one another, so much the more developed is the life of the animal in its various phænomena; or rather we should say, that the more various the separate manifestations of animal life, the more heterogeneous are the elementary parts by which that life is brought about.

It is the same with the separate divisions of an apparatus. The organization is higher when the divisions of a whole system or apparatus are less like one another and possess more individuality, than when a greater similarity pervades them. It is a higher grade of development, therefore, when the difference between the brain and spinal cord is greater, than when the original similarity is less disturbed. If we carefully discriminate between this relation of higher development and the relation of type, we shall readily overcome a multitude of difficulties which stand in our way, while we adopt the more or less generally predominating theory of a single continual line of progressive development from the Monad to Man. Let us take Fishes for an example. Because they possess a brain and spinal cord, together with an internal skeleton, and everywhere exhibit the great vertebrate type, they are raised above the heads of all the Invertebrata; and it is made a matter of wonderment that Bees, and the majority of insects which undergo a metamorphosis, exhibit more skill and a far more manifold vital activity. In Bees, however, nerves and muscles are far more differentiated than in Fishes. The single divisions of an apparatus or of an organic system are

also more heterogeneous. In most Fishes the stomach is but little distinguished from the intestine, nor this from the pyloric appendages. In the intestinal canal itself the large intestine is often hardly distinguishable from the small. The nervous system of Fishes presents a brain, which predominates but little over the spinal cord.

In the Bee we meet everywhere with more heterogeneity. The first coalesced pair of ganglia, although no actual brain, since we can only give this name to that part of the organism which forms the anterior extremity of a spinal cord, yet is far more pre-eminent over the rest of the nervous system than the brain of Fishes, and has more completely the signification of a centre of the nervous system. I believe, therefore, that the Bee is in fact more highly organized than the Fish, although upon another type*.

By *type* I mean the relative position of the organic elements and of the organs. This relative position is the expression of certain fundamental peculiarities in the direction of the vital activities, *e. g.* of the ingestive and egestive poles. The type is totally different from the grade of development, so that the same type may exist in many grades of development, and conversely, the same grade of development may be attained in many types. *The product of the grade of development with the type yields those separate larger groups of animals which have been called classes.*

The confusion of grade of development with the type of construction appears to me to be the origin of many failures in classification; and even in the obvious difference between these relations lies evidence enough that the different animal forms do not compose a single progressive series from the Monad to Man.

* It has long been observed, that, among allied forms, those which live in water, in the development of their animal, as contrasted with that of their plastic functions, are below those living on land, which exhibit more marked motor and physical capacities. May not the water be the cause of this? The antithesis of nerve and muscle appears not to be so decidedly developed in water as when there is a more active relation with the air. The muscles are softer and paler, the nerves are less white and consistent. We cannot get rid of the fancy that they both look as if they were infiltrated with water. When in Fishes certain muscles are remarkable for their redness, as the maxillary muscles of the Sturgeon, the nerves which supply them are whiter than the others.

I need follow out this remark no further; any closer examination will be rendered superfluous if I succeed in clearly explaining what I mean by type.

The type then is the relative position of the parts. It may be readily recognized that the different types are modifications of certain archetypes (*Haupt-Typen*), in which this relative position is especially characterized, and that intermediate forms occur which either unite the characters of the archetypes into a middle type, or in which one archetype preponderates in the one half of the body, in the other another. For the present I leave these intermediate forms out of consideration, referring to the essay which I have cited. But I must once again bring forward the archetypes in this place.

I believe that four archetypes may be clearly demonstrated,—the peripheral or radiate archetype, the articulate or longitudinal archetype, the massive or molluscous archetype, and the archetype of the Vertebrate*.

The peripheral type is exhibited by certain discoid Infusoria, by the Rhizostomidæ, Medusæ and Asteridæ. In their external form *superficial* dimension is represented. The principal antithesis is that of centre and periphery. The contrast of ingestion and egestion lies in a direction from the centre to the circumference. Hence the whole organization radiates from a centre. Besides this, the contrasted relation of upper and lower sides only is developed, and this slightly; no distinction of right and left, or of anterior and posterior, exists at all. Their movements are thence without definite direction. As the whole organization radiates from a centre, so the centres of all the organic systems are in the middle, or are disposed circularly around the middle (thus the stomach is in the middle, and round it are the nerves and vascular circlets, when these parts are developed at all); from them branches pass into the radii. In every radius is repeated what exists in any one; and every radius, if we follow

* I will not attempt to decide here, whether a peculiar type is not to be recognized in those animals whose whole organization is disposed not round a central point, but round an axis, as in the Holothuria. Ingestion and egestion are not here contrasted as centre and periphery, but as two ends of a line around which the remaining organization is peripherally disposed. Here too as a lower grade the Nematoidea might be arranged, and perhaps other lower forms.

it up to its centre, takes a similar share in the central parts also (the urinary system alone appears to make an exception), so that the whole body may be divided into a number of similar sectors, and the loss of a ray, so long as the middle remains uninjured, does not disturb life, since none of its necessary component parts are wanting.

In the longitudinal type, which obtains in the *Vibriones*, *Filariæ*, in *Gordius**, in the *Naidæ*, and in the whole Articulate series, the contrast of ingestion and egestion is relegated to the two extremities of the animal, and thus gives a character to the whole organization; the mouth and the anus are at the two ends, and in general the sexual organs also, yet at times these have their apertures more anteriorly. This is more frequently the case with the female organs, which are not merely egestive, but are also ingestive, than with the male organs. When the organs of both sexes are removed from the posterior extremity, the aperture of the female organs generally is placed more forward than that of the male organs. It is thus in the Myriapoda and the great family of Crustacea; the Leech and the Earthworm form a rare exception. With the fixed position of the anterior extremity, as the ingestive pole, the organs of the senses as instruments for the receptivity of the nervous system early attain a considerable grade of development.

So long as the type remains unchanged, the intestinal canal passes straight through the body. It is the same with the vascular and nervous systems. Every organic movement then has this principal direction, only subordinate branches pass off laterally; especially when the principal character is repeated along the whole length, as in a galvanic battery, so that every separate segment possesses its own anterior and posterior extremity, together with its portion of the essential constituents of the organism.

Thence the disposition to break up into many portions in the direction of the length of the body. In the true Insects possessing metamorphosis, these articulations are united again into three principal sections, in the first of which the nervous, in the second the motor, and in the third the digestive life predomi-

* If these animals, or some of them, are not perhaps in accordance with the previous note, to be brought under one type with the Holothuriadæ.

nates, although in each of the three segments none of these is wholly absent.

Together with the principal contrast of anterior and posterior, a slighter one of upper and lower is to be recognized in the higher stages of development. A distinction into right and left sides is only exceptionally present, and as a rule is absent. A perpendicular plane therefore divides the body into two equal halves, whence this organization may be called symmetrical. Every single organ lies in this middle plane, so long as the shortening of the whole body does not drive the less shortened intestine out of the median plane*; and every organ which lies in the median plane is single, while that which lies external to it is double. In the median plane, however, we must recognize a difference of above and below; the animal organs are concentrated below, the plastic ones above, if we regard only the internal structure. The trunks of the animal organs also lie below, and they form here a kind of axis, from which the whole organization proceeds on both sides upwards,—a relation which is rendered obvious by the mode of development (compare Coroll. 4).

The sensible and the irritable functions are especially developed in this series of animals; their movements are lively, and are the more distinctly directed forwards the more the body is drawn out longitudinally. When the body is shortened, as in the Spiders and Crabs, so much the less determinate is the direction of their movements; the plastic organs are less developed, the glands are particularly rare, and are generally replaced by simple tubes.

I believe that a third type is recognizable in the Mollusca; and as belonging to its lower grades of development I enumerate the Rotifera and such Infusoria as are coiled, or at least are neither symmetrical nor peripheral. This type may be called the *massive type*, for neither length nor surface predominates, but the whole body and all its parts are formed in more rounded masses, which are either solid or hollow.

As the principal antithesis of animal organization, that of ingestion and of egestion, is manifested neither by the two opposite

* In fact, it appears that in Insects which possess metamorphosis, the intestine is moved out of the median plane, sometimes only in the last stage of metamorphosis, sometimes even in the larval condition

ends of the body nor by the centre and periphery, it is almost always wanting in symmetry; the egestive pole lies almost always to the right of the ingestive pole. The opposite relation is so rare, that it has been called inverted. On the other hand, the egestive pole is sometimes very near the ingestive one, sometimes is removed far from it, so that it approximates the posterior end of the body. Since the digestive track is always determined by these two poles, it is more or less curved. In its simplest form the track is simply looped, as in *Plumatella*. When the alimentary canal elongates, it rolls up spirally in the middle, and the spiral apparently follows determinate laws. The commencement of the intestinal canal thus appears always to lie under the portions which follow.

The main current of the blood follows a curve which does not lie in the middle line of the animal. If the spiral of the intestine be wound in one plane, a certain symmetry is so produced, as in the discoidal univalves and the equivalve bivalves; but this symmetry is only very unimportant, and it might be called almost accidental, since it is often wanting in nearly allied animals.

The nervous system is composed of scattered ganglia, which are united by filaments into a network. The larger ones are collected round the pharynx. The psychical apparatus is very little developed, and the organs of sense are late in arising. Motion is very slow and weak. From the absence of articulation, the muscles are interwoven in all directions, and operate upon every point by single bundles; thence arise contractions in all directions. Since, in accordance with the massive archetype, the secretory organs, which in other archetypes appear as tubes, coil up in this, the glands are abundant and large. The plastic organs in general are those which are earliest and most completely developed; and thence this archetype might also be called the *plastic* archetype. Since it possesses neither lateral nor peripheral equivalency, the body can be divided into similar segments neither in one nor in many planes. Neither can any straight axis be demonstrated in it round which the organization is distributed; it is rather determined by manifold curves.

In the Vertebrata we find a fourth archetype. It is, however, in a manner constructed out of the preceding archetypes. We

can distinguish, that is, a plastic and an animal part of the body, which react mutually upon one another's form, but each of which is modelled upon a different archetype. In the animal part, the existence of articulation calls to mind the second archetype; ingestion and egestion are similarly referred to the two ends. But there is an essential difference; the animal part of the vertebrate animal, namely, is not merely double on each side of a longitudinal axis, but also from above downwards, and in such a manner that the two inferior lateral developments enclose the plastic organs, while the two superior include central organs of animal life (spinal cord and brain), which are wanting in the Invertebrata. The solid bony skeleton represents this type most completely; from a median axis, the trunk of the vertebral column, arches pass upwards, which unite in a superior crest, and other arches downwards, which more or less unite into an inferior crest. Corresponding with this, we have four series of insertions of nerves into the spinal cord, which again contains four principal cords, and a four-lobed internal gray mass. In the same way, the muscles of the trunk form four principal masses, as we see most distinctly in Fishes. The animal part, therefore, is doubly symmetrical in its construction.

Here, as in the essay in the '*Nova Acta*' already cited, I will not decide whether, in the course of the further development of the Vertebrata, the anterior part of the animal region approximates more and more to the radiate archetype; I would only suggest, that the brain accumulates more and more round the third ventricle, and that the cerebral vessels also pass into the brain from a ring, which becomes continually more and more rounded, although this ring is fed by four vascular trunks, as representing a relation, such, that from a type in which the parts were originally arranged in fours, a radiate one is developed.

However, it appears to me to be more readily demonstrable, that the type of the Mollusk predominates over the plastic part of the body, although everywhere under the influence of the animal part, by which the type is sometimes more, sometimes less obscured.

The plastic nervous system, as well as the peculiarity of the plastic muscular system, calls to mind the molluscous type.

But the chief matter is to demonstrate that the most essential peculiarity, the direction of the vital organic current, has a prevailing tendency towards the right side. If now this lateral contrast does not manifest itself in the ingestive and egestive apertures, the reason perhaps lies in this, that the plastic body is surrounded by the animal body; and, therefore, when the former comes to the surface, it is wholly subjected to the type of the latter. The mouth and the anus therefore lie in the median plane of the whole body*.

If we turn to the internal organs, we must not forget that,—

1. Almost all organic progression is followed by a retrogression. Were this not the case, a few beats of the heart would drive all the blood out of the body. The question here then is only to state what is the direction of that movement which is the determining one.

2. That in other cases also the motion can be withdrawn from the direction which originally belongs to it if it possesses a starting-point, which according to the laws of the organization is also the termination of another more powerful organization.

3. That by the symmetrical influence of the animal part, a current is set up in the median plane of the plastic part. Then if we find a movement at times external to this plane also, but always taking the same direction, we should consider this as the original one.

These remarks will be rendered more clear by the application which will immediately be made of them.

If, in the first place, we consider the movement of the blood, we find that in Fishes its principal stream proceeds in the median plane out of the heart, without doubt only on account of the predominance of the animal part, in which respect we must refer to a remark to be made concerning the respiratory apparatus.

And yet it would seem even here as if the blood desired to go towards the right side, for the ventricle of Fishes appears in general to be more extended towards the left side, and the auricle also lies towards the left. The direction which the blood thence receives is somewhat to the right, but the symmetrical structure of the gills keeps it back in the median plane. In all animals

* Yet in the larva of the Frog, the anus lies in fact on the right side of the median plane of the tail.

with lungs, however, the stream of the blood passes obviously more to the right than to the left side; so that for the nutrition of the left half of the head, the blood must often come over from the right side. This blood then has a motion from right to left, which we must regard as a consequence of symmetry in the animal part. It is unquestionably the left ventricle which is the chief agent in propelling the blood, and this always sends the blood to the right side. In the Lizards, Snakes, and Chelonia, all the blood which is intended for the nutrition of the anterior half of the body passes first in a single stream to the right side, and then becomes distributed; the blood for the anterior extremity now passes forwards almost symmetrically in two streams; the blood intended for the posterior extremity in Birds continues its course without dividing to the right side, and by degrees, as the influence of symmetry gradually weakens that of the motor power, it turns leftward again, so as to reach the median line. In the Amphibia above mentioned, the power of symmetry sooner becomes manifest; the current of blood for the posterior half of the body is also divided at the first, but much more blood passes to the right than to the left side, and the latter becomes sooner divided, as if it were propelled with less force. In the Batrachia, the distribution is from the first tolerably symmetrical. In Mammalia, the aorta descends indeed upon the left side of the vertebral column; but if we consider that the position of the aorta is always determined by a large and common trunk for the anterior and posterior arteries, that this common trunk is always directed towards the right side, and first becomes turned to the left after it has given off the arteries of the right anterior half of the body, or gives them off as it turns; the passage to the left side may be regarded as arising from the influence of symmetry, for the arch which the aorta forms is the wider the shorter the neck. In other words, the aorta passes the more to the left side, the nearer it stands to the head whose influence tends towards symmetry. In the long-necked Mammals, where from the common trunk upon the right side, that for the carotid artery and subclavian arteries (the anterior aorta) passes, the branch which passes backwards turns so suddenly that it can hardly be said that it passes to the left.

Such considerations may perhaps explain why it is that the

Mammalia differ from other pulmonated Vertebrata in the position of their descending aorta. I believe that this difference depends upon the greater need of blood demanded by their brain. Let us consider, in some indifferent vertebrate animal, the stream of blood passing from the left ventricle to the right side. If the brain have a great demand for blood, this common stream of blood, besides its direction to the right side, will take at the same time a more forward direction than in animals with a small brain and head. In the latter, therefore, the blood which is intended for the posterior half of the body, after giving off the blood to the anterior half, is by the influence of the current immediately bent backwards, though continued for a little to the right side. If, however, the current forward be more powerful, the backward stream can only gradually overcome it, and the aorta needs to pass further forwards, and to the right side; or if the influence of symmetry will not allow of this, it must bend round to the left in order to pass backwards. That the blood in the Mammalia actually has a more powerful current forwards, is indicated by the greater length of the common trunk; and the fact that among the Mammalia again, the longer this common trunk is the wider the arch, is perhaps a confirmation of what has been said. In this way we may conceive the origin of the difference in a formless mass. How it is developed out of the symmetrical branchial apparatus of the Mammalia remains to be decided by future investigations.

Even when the heart lies in the median plane of the body, the origin of the aorta, as soon as there are two ventricles, is always so disposed that the impulse which is given to the blood by the left ventricle passes to the right side. When the point of the heart turns to the left, this relation is still more marked (see figure on p. 238, arrow 1). A direction of the heart towards the right side never appears to be normal. I believed that I had at times observed it, but I persuaded myself that this position arose only from a slipping about in the body of the animal inverted for the purpose of examination. We may therefore be permitted to place the heart in such a manner in our diagram as it is disposed in Man and some other animals*. I choose the oblique position

* It would seem that the symmetrical position of the heart is too generally ascribed to quadrupeds. It appears to me to occur only in animals with a

of the heart, in order to show by it how the strong development of the currents in a predominant organ may produce an opposite current in a dependent part of the same system. In most animals the pulmonary blood flows straight backwards into the left heart; where, however, this is placed in such a manner that it propels decidedly towards the right side, the current of pulmonary blood takes a slight direction to the left side (1′).

So much for the direction of the arterial current. That the venous current is also directed towards the right side is much more obvious. The blood from the left side of the anterior half of the body passes very markedly towards the right side. We may therefore at once indicate the course of the venous blood from the anterior part of the body by the arrow 2. That the blood from the posterior part of the body also moves towards the right side is shown by the deviation of the posterior vena cava to the right the further forwards it passes, as well as by the conformation of the intercostal trunks; the arrow 3 represents this current. It is still clearer in the portal system (4). If we cast a glimpse over the whole series of animals, we find the respiratory system sometimes connected with the ingestive, sometimes with the egestive end of the body, sometimes disposed longitudinally between the two extremes. This variety of position appears to be possible to the respiratory apparatus, because its function is as well excretory as ingestive. One is tempted to suppose that in those forms of animals in which the respiratory apparatus occupies the anterior extremity, it acts more ingestively; while, on the other hand, it is more egestive in those in which it opens together with or near the intestine, as in the Holothuriadæ, most Mollusks, and some larvæ of Insects. If we extend this supposition to the changes undergone by the blood itself, it must still remain hypothetical, for at present in very few animals only can we determine whether the blood loses or gains substance during respiration. It appears to me, however, to be very clear, that in those respiratory apparatuses which are placed anteriorly, the *ingestive movement* at least is the deter-

compressed thorax. In animals with a flattened thorax, the heart lies more or less obliquely, and in the embryonic condition sometimes more so than in the adult. Thus, recently, in many embryo Hedgehogs, I found the heart directed very markedly towards the left side, while it was much less so in the mother.

mining one, while in those which are situated posteriorly it is the egestive movement. In the Holothuriadæ, the Mollusks, the larvæ of Insects which inhale air by their hinder extremities, the respiratory organs are emptied by muscular contractions. The refilling is principally a consequence of the cessation of muscular activity; at least, if an antagonistic muscular action be superadded, it is less than the expelling force. The reverse takes place in the pulmonated animals; the reception of air is here more active, its expulsion is more passive. The inhalant passage will therefore determine the position of the apparatus, not the retrogressive passage of the exhaled air. Now, though we find the lung double, yet in all animals the right lung is larger, and in the true Ophidia it is this alone which is developed, a trace only remaining of the left. To this may be added, that in some Cetacea, as in the genus *Physeter*, the right nostril is dwarfed. Indeed it may obtain even more generally that the right nasal aperture is smaller than the left, as we see for example in Sömmering's description of the skull of the fossil Hyæna. We may then shortly indicate the course of the air in the respiration of the Vertebrata by the arrow (5) in our figure (p. 238). In the gills of Fishes it must be admitted that no such lateral difference is apparent; but the gills are so immediately connected with the animal part of the body, as the transitory gill-arches of the pulmonate animals testify, that the asymmetry of the plastic body cannot develope itself in them.

When an apparatus like the digestive passes from one pole to the other through the whole length of the plastic body, it certainly cannot send its contents always to the right side. It is only to be expected, that in those sections in which the motor powers are most strongly manifested, which are therefore those which determine the position of the whole, the course of the current will be in this direction. Now we find in all Vertebrata, so far as I know, that the stomach lies to the left and the pylorus to its right side, as well as the commencement of the duodenum, turning to the right whether it pass at the same time forwards or not. The stomach therefore propels its contents towards the right side. The same relation is frequent in the muscular rectum. Other sections must indeed pass from right to left, but they are the less active. Thus I conceive that if the food in

Mammals passes to the left in order to reach the stomach, this opposed direction is only produced by the influence of the stomach, which, in order to propel to the right, lies towards the left. It is also only the posterior part of the œsophagus which is overruled by the stomach; for when the bony skeleton of the neck is so much bent that the œsophagus passes away from its under surface, the œsophagus always, if I err not, lies on its right side with the exception of its posterior extremity. I found its position thus in Birds, in Chelonia, in the Camel, in the Sloth, and probably in many other Mammals the same holds good. When in Birds a special crop is developed, this also is placed upon the right side. The course of the motion from the pharynx, therefore, which is produced by the powerful constrictors, is in general towards the right side. Compare arrow 6*.

The course of the bile generally is from the right to the left; but this reversed direction may be regarded as dependent upon the position of the liver, which is thrust to the right side in consequence of the predominant current of the portal blood. In fact, in the course of embryonic development, the liver passes to the right side in proportion to the separation of the portal system from the other vessels.

As respects the sexual organs, they are as a rule tolerably symmetrical, in consequence of their intimate connexion with the animal body, which is rendered evident not only by their position in the adult, but especially by the history of development. Where, however, symmetry is less prominent, as for example in the hen-bird only, the left oviduct is developed, and the egg therefore is moved from the left towards the right side. The direction of this movement is exhibited by the arrow 8. Hitherto all the arrows which have been drawn have their points directed towards the right side. The urinary passages only appear not to harmonize with this law. When the kidneys upon the two sides do not agree, as in the Ophidia, it is that of the right side, which is longer and placed more anteriorly. The

* That the passage from right to left again is submitted to a determinate standard, that therefore a definite form of spiral canals might be demonstrated when the current cannot be continued to the right side, scarcely admits of doubt. Yet here the perturbations are so frequent, and the discovery of the type is so difficult, that this attempt would carry us too far. Besides, I consider the current to the right to be that which is predominant and common to all systems, and for our present purpose it is sufficient.

course of the urine would then seem especially to be towards the left. If the principal activity of the kidneys should consist in attracting venous blood, merely allowing the urine to transude, they would come under the general law*.

Enough of the demonstration that the organic current in the plastic part of the Vertebrata has a direction especially towards the right side, in order to show that the arrangements of the molluscous type prevail in this half of the vertebrate animal.

We have now considered the four archetypes, and it will be sufficient for our purpose to remark shortly, that these archetypes become modified in the subordinate forms, like the variations of one theme. Thus the segments of the Articulate series sometimes more resemble one another, as if they were strung upon a thread, sometimes they are collected round a central point. In this manner variations of the archetypes are formed, which may be conceived to be arranged round them, and some of which are more nearly approximated to them, representing more purely the character of the archetype, while others are further removed. These subordinate types, combined with a determinate degree of development, yield what we call the classes of animals. In these it is sometimes one, sometimes another vital condition which is more developed; or more justly, the development of life in this or that direction produces the variations of the archetypes, just as these are themselves essentially different in the vital phænomena which they manifest. Thus among the Vertebrata it is plainly the Birds, in which the relation to the air is predominant. It penetrates their whole body, and for it the anterior motor organs are constructed. So with the true winged Insects among the Articulata. The classes of animals again are divisible into smaller variations, which we call families, in which not only the archetype but the type of the class is exhibited, together with peculiar modifications which constitute the character of the family. Smaller modifications in this family character yield the genera. And so it goes on down to the species and subspecies.

* The preponderance of the right kidney is not universal even in the Snakes. At times their length is balanced by the greater thickness of the left kidney, as I observe in *Vipera Berus*. In *Tortrix Scytale*, however, the preponderance of the right kidney is, I find, according to Meckel and Finke, evident. It is remarkable that the urinary system is the only one which is aberrant in the peripheral type also.

If it be true that all the larger and smaller groups of animals depend upon a double relation, that of higher or lower development, and that of the variation of the archetypes into differences of smaller degree, and these again further, then the conception of a uniserial progressive development of the whole animal kingdom is incorrect.

§ 4. *Application of this View to the History of Individual Development.*

Let us now apply the survey of the permanent relations of form among the various perfect animals to the history of the development of the individual!

Before all things it is clear, that the conditions which we have termed the higher and lower development of the animal, coincide perfectly with that histological and morphological differentiation which gradually arises in the course of the development of the individual (comp. Schol. III. *c. d.*). In this respect the agreement is striking. The fundamental mass of which the embryo consists agrees with the mass of the body of the simplest animals. In both the form is but little defined; the parts are less contrasted, and the histological differentiation remains even behind the morphological. If we cast a glance over the lower animals, remark in some more internal development than in others, and then arrange them in a series according to this development, or conceive them to be developed out of one another; it necessarily follows that we should trace an agreement in *the fact of this very progressive differentiation* between the one actual historical succession and the other imagined genetic series; and in this manner a multitude of coincidences may be demonstrated between the embryo of the higher and the permanent forms of the lower animals.

It by no means follows from this, however, that every embryo of a higher animal gradually passes through the forms of the lower animals. On the contrary, the type of every animal appears to be fixed in the embryo from the very first, and to regulate the whole course of development.

All that we have stated with regard to the development of the Chick is only a long commentary upon this proposition. The chorda dorsalis is the first part which becomes differentiated.

From this the dorsal plates elevate themselves, and the abdominal plates soon arise, and the spinal cord becomes separated. All these formative processes take place very early; and it is obvious that henceforward there can be no question of any agreement with an invertebrate animal; that, on the other hand, those conditions which essentially constitute the vertebrate animal are the first to arise; the commencement of their development is however very similar in all classes of the Vertebrata. We may therefore say, not merely of Birds, but more generally,—*The embryo of the vertebrate animal is from the very first a vertebrate animal,* and at no time agrees with an invertebrate animal. A permanent animal form, however, which exhibits the vertebrate type, and yet possesses so slight a histological and morphological differentiation as the embryos of the Vertebrata, is unknown. *Therefore, the embryos of the Vertebrata pass in the course of their development through no (known) permanent forms of animals whatsoever.*

Can, however, no law be discovered to regulate the development of the individual as the possessor of a special organic form? I believe there can, and I shall endeavour to educe it in the course of the following remarks. The embryos of Mammalia, of Birds, Lizards and Snakes, probably also of Chelonia, are in their earliest states exceedingly like one another, both as a whole and in the mode of development of their parts; so much so, in fact, that we can often distinguish the embryos only by their size. In my possession are two little embryos in spirit, whose names I have omitted to attach, and at present I am quite unable to say to what class they belong. They may be Lizards, or small Birds, or very young Mammalia, so complete is the similarity in the mode of formation of the head and trunk in these animals. The extremities, however, are still absent in these embryos. But even if they existed in the earliest stage of their development, we should learn nothing; for the feet of Lizards and Mammals, the wings and feet of Birds, no less than the hands and feet of Man, all arise from the same fundamental form. The further, therefore, we recede in tracing the formation of the Vertebrata, the more similar we find the embryos in their totality and in their separate parts. At first those characters gradually present themselves which indicate the greater, and

subsequently those which mark the smaller, divisions of the Vertebrata.

Thus the more special type is developed from the more general. Every step in the development of the Chick testifies to this. In the beginning, when the dorsal folds have closed, it is a vertebrate animal, and nothing more. As it raises itself from the yelk, as the gill-plates coalesce and the allantois grows forth, it shows itself to be a vertebrate animal, which cannot live freely in water. Subsequently the two cæca grow forth, a distinction appears between the pairs of extremities, and the beak is developed; the lungs pass upwards; the rudiments of the air-sacs are recognizable, and there can be no doubt as to its being a Bird. While the ornithic characters become more and more marked, in consequence of the further development of the wings and air-sacs, of the coalescence of the tarsal cartilages, &c., the web of the feet disappears, and we recognize a land Bird. The beak, the feet, pass from the general into a special form; the crop is developed, the stomach has already divided into two cavities, and the scale of the nostrils appears. The Bird takes on the character of a Gallinaceous bird, and finally of a domestic fowl.

It is an immediate consequence, in fact it is merely a changed form of expression of what has been said above, that *the more different two animal forms are, so much the further back must their development be traced, to find them similar**. To demonstrate that this is true, not merely for the Vertebrata, we will select a few examples from the lower animals. The difference between the Macrurous and Brachyurous Crustacea is not very great. Now the river Crayfish has at the middle of its embryonic life a tail tolerably short in relation to its broad thoracic segments, and it can be hardly distinguished from a Brachyurous Crustacean, since, according to Cavolini's representation, these have in their embryonic condition tolerably long tails. The further we trace them back, the more similar do we find the jaws in Crustacea to the feet; in truth, they are at first the anterior feet, and nothing else. We have therefore not only an approximation to the fundamental type (agreement of allied organs), but also a similarity with the Stomapoda, Amphipoda

* This remark does not invalidate what has been said in the First Scholium as to the indefiniteness of the same form in its earliest condition.

and Isopoda, which in their perfect condition are far more different from the Decapoda than these from one another. To this it must be added, that, according to Rathke, the heart in the Decapoda (*Isis*, Bd. xvii. p. 1098) is at first fusiform, and doubtless there are many more points of agreement as yet undiscovered.

At a still earlier period, when the feet sprout forth at the sides like little knobs, and no gills are as yet visible, we cannot mistake the similarity to true Insects in the larval state. A Butterfly and an Ichneumon may be readily mistaken for one another even as full-grown larvæ. Such larvæ have indeed been compared with Vermes, but it must be confessed that the essential differences are still very great. The latter have red blood and no tracheæ. In the former the reverse obtains. In fact, the full-grown caterpillars are much more similar to the Myriapoda, and only at a very early period, when no tracheæ are developed (these being probably formed by histological differentiation), is there any approximation to the embryo of the Leech when it has not yet developed red blood.

These remarks lead us to inquire, whether by going further and further back, we may not eventually attain a stage in which the embryos of the Vertebrata agree with those of the Invertebrata. In a future essay, in which the differences in the schemes of development in the principal types of animals will be treated of, I shall endeavour to show that the Articulate series also commences its development by a primitive streak. For this short period, therefore, there would be an agreement between them and the Vertebrata. In the condition of the actual germ, however, it is probable that all embryos which are developed from true ova agree. This is a strong reason for considering the germ as the animal itself (Schol. II.). When in the germ of the Bird the primitive streak is developed, we are indeed inclined to say, Now commences the embryo. But in reality this is only the *instant in which the vertebrate type appears in the germ*; for the primitive streak is nowise the whole embryo, inasmuch as the parts which are metamorphosed into the abdominal plates evidently lie beside it in the germ. It is only that part of the germ which first becomes individualized. A so-called germinal disc is however distinctly visible in the ova of the Articulata. It is almost certainly present in the Mollusca, for the ovum of

Gasteropods has an unequal coloration upon its surface. Besides I have seen clearly the germinal layer and the germinal vesicle, the predecessors of the germ. It therefore seems to me very probable that all true ova have a distinct germ.

The further back we trace development, so much the more agreement do we find among the most widely different animals, and thus we are led to the question,—Are not all animals essentially similar at the commencement of their development—have they not all a common primary form? We have just remarked, that a distinct germinal disc probably exists in all true ova; so far as we are acquainted with the development of germ-granules (*Keim-körner*), it seems to be wanting in them. They appear to be originally solid; however it may be, that on their first separation from their parent, they have an internal cavity like the central cavity of the yelk, which only escapes microscopic observation on account of the thickness of the often somewhat opake wall. Supposing, however, they are at first solid, and eventually become hollow, as seemed to me to be the case with the germ-granules of the Cercariæ and Bucephali*, yet we perceive that the first act of their vital activity is to acquire a cavity, whereby they become thick-walled, hollow vesicles. The germ in the egg is also, according to Schol. II. c, to be regarded as a vesicle, which in the Bird's egg only gradually surrounds the yelk, but from the very first is completed as an investment by the vitellary membrane; in the Frog's egg it has the vesicular form before the type of the Vertebrata appears, and in the Mammalian from the very first it seems to surround the small mass of the yelk†. Since, however, the germ is the rudimentary animal itself, it may be said, not without reason, that the simple vesicle is the common fundamental form from which all animals are developed, not only ideally, but actually and historically. The germ-granule passes into this primitive form of the independent animal immediately by its own power; the egg, however, only after its feminine nature has been destroyed by fecundation (compare the Coroll. to Schol. I.). After this influence, the differentiation of germ and yelk, or of body and nutritive substance, arises. The excavation of the germ-granule is nothing

* *Nova Acta Acad. Nat. Cur.* vol. xiii. T. 2. p. 658.

† Heusinger's *Zeitschrift für organische Physik*, Bd. ii. p. 173.

else. In the egg, however, there is at first a solid nutritive matter (the yelk), and a fluid in the central cavity; yet the solid nutritive matter soon becomes fluid.

We remarked above, that to find a correspondence between two animal forms, we must go back in development the further the more different these two forms are; and we deduce thence, as the law of individual development,—

1. *That the more general characters of a large group of animals appear earlier in their embryos than the more special characters.*

With this it agrees perfectly, that the vesicle should be the primitive form; for what can be a more general character of all animals than the contrast of an internal and an external surface?

2. *From the most general forms the less general are developed, and so on, until finally the most special arises.*

This has been rendered manifest above by examples from the Vertebrata, especially of Birds, and also from the Articulata. We bring it forward again here only to append, as its immediate consequences, the following propositions concerning the object of investigation:—

3. *Every embryo of a given animal form, instead of passing through the other forms, rather becomes separated from them.*

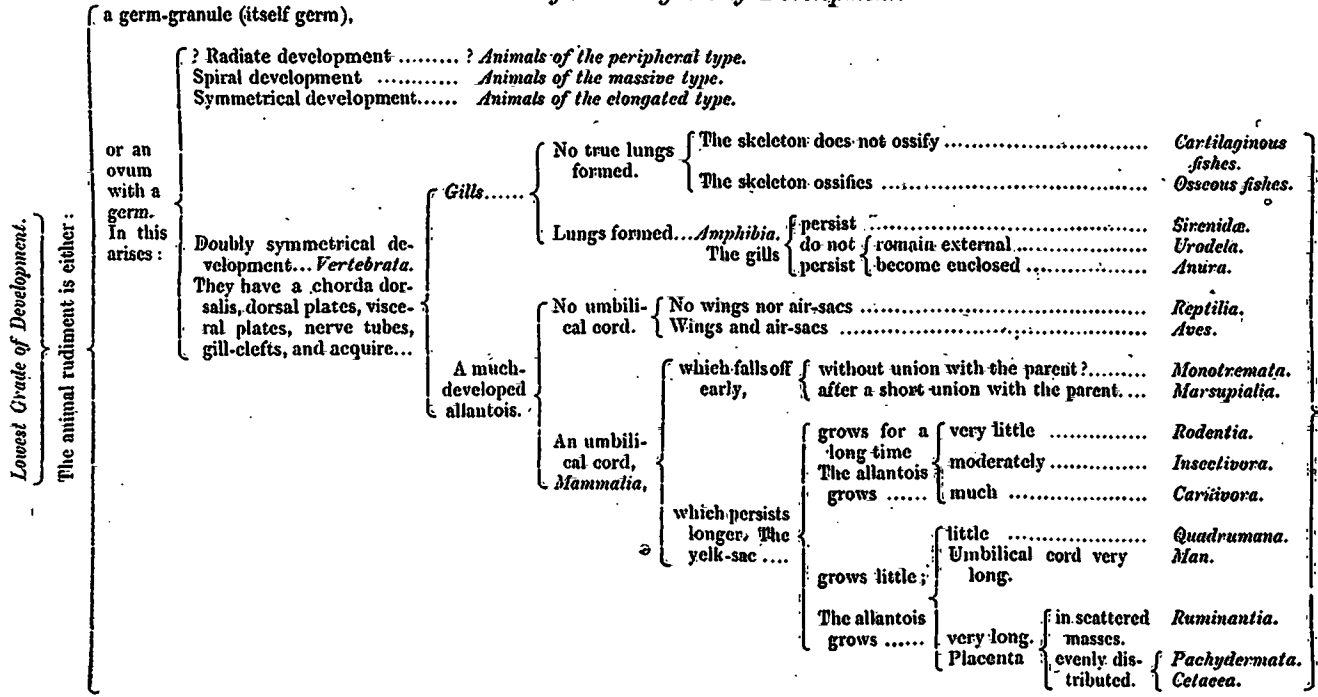
4. *Fundamentally, therefore, the embryo of a higher form never resembles any other form, but only its embryo.*

It is only because the least developed forms of animals are but little removed from the embryonic condition, that they retain a certain similarity to the embryos of higher forms of animals.

This resemblance, however, if our view be correct, is nowise the determining condition of the course of development of the higher animals, but only a consequence of the organization of the lower forms.

The development of the embryo with regard to the type of organization, is as if it passed through the animal kingdom after the manner of the so-called *méthode analytique* of the French systematists, continually separating itself from its allies, and at the same time passing from a lower to a higher stage of development. We represent this relation by the annexed Table:—

Scheme of the Progress of Development.


Lowest Grade of Development.
Highest Grade of Development.
The animal rudiment is either :
a germ-granule (itself germ),
or an ovum with a germ.
In this arises :
? Radiate development ..... ? Animals of the peripheral type.
Spiral development ..... Animals of the massive type.
Symmetrical development..... Animals of the elongated type.
Doubly symmetrical development... Vertebrata.
They have a chorda dorsalis, dorsal plates, visceral plates, nerve tubes, gill-clefts, and acquire...
Gills.....
No true lungs formed.
The skeleton does not ossify ..... Cartilaginous fishes.
The skeleton ossifies ..... Osseous fishes.
Lungs formed... Amphibia.
The gills persist ..... Sirenidæ.
do not persist: remain external ..... Urodela.
become enclosed ..... Anura.
A much-developed allantois.
No umbilical cord.
No wings nor air-sacs ..... Reptilia.
Wings and air-sacs ..... Aves.
An umbilical cord, Mammalia,
which falls off early,
without union with the parent?..... Monotremata.
after a short union with the parent.... Marsupialia.
which persists longer. The yelk-sac ....
The allantois grows ..... long time
very little ..... Rodentia.
moderately ..... Insectivora.
much ..... Carnivora.
grows little;
little ..... Quadrumana.
Umbilical cord very long. Man.
The allantois grows ..... very long.
Placenta in scattered masses. Ruminantia.
evenly distributed. Pachydermata.
Cetacea.

In detail it holds good as little as any other representation of organic relations upon a surface. Thus the single features adduced must pass for the whole characters, *e. g.* the formation of wings and air-sacs for the whole character of Birds. The exposition, again, can only be very imperfect, since for most animals the investigation has hardly been commenced.

This scheme is only meant to bring clearly before the mind, how the first decisive distinction is whether the first rudiment is a true egg or a germ-granule; how, in the germs of ova, all animals are at first alike (see above, *e*); how then the principal type becomes defined (which is called, origin of the embryo); whereby it remains undecided whether any radiate animal is developed from a true egg. If now the type of the vertebrate animal appears, the embryo is at first nothing but one of the Vertebrata without any particular characteristics. Chorda dorsalis, dorsal and abdominal tubes, gill-clefts, gill-vessels, and a heart with a single cavity, are formed in all. Then commences a differentiation. In a few, gill-laminæ and no allantois are developed; in others, on the other hand, the gill-clefts coalesce, and an allantois buds forth. The former are aquatic animals, though not all permanently so: the others lead an aërial existence. The latter all acquire lungs. Let us follow out the former series first however. The embryos for a long time retain a great similarity; they push out long tails and scull about with them in the water. On the other hand, their extremities are developed very feebly and late, in relation to those of other embryos. They either never acquire true lungs, and so become fish, or else true lungs are formed. Among the latter the lungs are either feebly developed, in which case the gills are permanent and the animals become Sirenidæ; or the lungs are better formed, and the gills either remain free until they cease to act (Salamanders), or they become covered over, the tail disappears, and with it all resemblance to a fish (tail-less Batrachia). In the second series of the Vertebrata, which never has external gills, the most essential distinction is perhaps this,—that in some a simple umbilicus is formed (Reptiles and Birds), in others this umbilicus is prolonged into a cord, after, as it seems, being altogether more rapidly formed (Schol. II. *b*.).

In what manner Birds become separated from the Amphibia

has already been shown. Probably a difference also arises very soon in the vascular system, whose metamorphoses in the Amphibia, however, are not yet known. While the gill-clefts in the Lizards are still open, the heart has just the same appearance as in Birds at the same period. Now just as in the Bird the special characters of the family and of the genus arise, so is it in the Mammalia. The Dog and the Pig are at first very much alike, and have short human faces. Still longer does the resemblance persist between the Pig and the Ruminant, whose lateral toes are at first almost as long as the two median ones. For the rest we are by no means sufficiently acquainted with the embryos of the Mammalia to state how and at what periods they become distinguishable from one another. We are best acquainted with the differences in the form and structure of the ova. Since these are very manifold in their form and in their relation to the parent, I have ventured, in order not to leave the Mammalia out of the Scheme, to divide them according to their ova. The embryos, in fact, may be distinguished into those which are born early and those which come into the world in a fully developed condition. Among the former the ova of the Monotremata are probably born undisturbed. In the Marsupialia the embryo has burst its membranes. The ova, which are retained longer, may be reduced to three principal divisions. In the first I place ova, in which the yelk-sac continues to grow for a long time. They yield Mammals with narrow hook-like nails (claws). In some the allantois is early arrested in its growth, and the placenta is limited to one spot, or two-lobed* (Rodentia). In others the allantois is developed to a moderate extent (Insectivora): in all others it grows over the whole amnion transversely, and the placenta is annular (Carnivora). A second division of long-retained ova is formed by those in which the yelk-sac and the allantois are small; the placenta is one-sided, and is, as it would seem, in the opposite position to that of the Rodentia; the amnion and the umbilical cord are here

* I must for the present follow Cuvier in stating that in the Rodentia the allantois remains very small, since in my earlier investigations I did not pay sufficient attention to this point, and for the last three months I have endeavoured in vain to obtain pregnant Rabits. The allantois is moderately large in the Hedgehog (one of the Insectivora), as I have recently observed.

largest. These ova produce animals with flat nails and three-lobed cerebral hemispheres*. A third division has a yelk-sac which soon disappears, but an allantois which grows out immensely at its two extremities. These ova produce ungulated and finned animals; if the placenta is distributed over the whole ovum, but is collected in particular masses, we have animals with cleft hoofs; if it is distributed homogeneously, we have other Ungulata and Cetacea†. Hence the principal differences of the Mammalia are marked very early in the ovum, for according as the allantois is much developed, or otherwise, does the ovum become long or short‡. In the former case, the embryo not only acquires a broader horny covering upon its fingers, but also a more complex stomach, and, in connexion therewith, long jaws, a flat articulation of the jaw, usually complex teeth, incapability of seizing and climbing, &c. &c. It is the *plastic* series among the Vertebrata.

I must advert to an objection against the whole view here set forth, which may be based upon the circumstance that in some cases the embryos of nearly allied animals exhibit considerable differences at an early period. The embryos of the Ophidia, for instance, are very early rolled up, and so may be readily enough distinguished from Lizards. This plainly arises from the excessive length to which in this case the vertebrate type is drawn out.

Dissection, however, exhibits a great harmony in the internal structure; and since the posterior extremity of the Lizards also forms a spiral, the difference probably lies merely in this, that the vertebrate type in the Ophidia is more elongated, and it *seems*, in fact, to be greater than it *is*, because it presents itself so nakedly. Thus also the larvæ of many families of Insects are in their external appearance very different in different families. Much probably depends in this case upon their shorter or longer sojourn in the egg. However, this objection, the only one which

* It would be very interesting to know the ova of the Lemurs, so as to ascertain whether they are very similar to those of the Monkeys or not.

† According to a letter of Rudolphi's, the chorion of the Dolphin is similar to that of the Horse. According to Bartholin it is a *placenta exilis*.

‡ Perhaps the difference may be recognized still earlier in the chorion. See *Ueber die Gefässverbindung zwischen Mutter und Frucht*. Leipzig, 1828, fol.

I have been able to discover against the view in question, can have little weight so long as no internal differences in the larvæ have been demonstrated.

For the simple reason, that the embryo never passes from one principal type to another, it is impossible that it can pass successively through the whole animal kingdom. Our Scheme, however, shows at once that the embryo never passes through the form of any other animal, but only through the condition of indifference between its own form and others; and the further it proceeds, the smaller are the distinctions of the forms between which the indifference lies. In fact, the Scheme shows that the embryo of a given animal is at first only an indeterminate Vertebrate, then an indeterminate Bird, and so forth. Since at the same time it undergoes internal modification, it becomes in the whole course of its development a more and more perfect animal.

However, it may be objected here, if this be the true law of development, how comes it that so many good reasons could be adduced for that which has been previously in vogue? This may be explained readily enough. In the first place, the difference is not so great as it looks at first sight; and in the second, I believe that an assumption was made in the latter view, and it was afterwards forgotten that it had not been demonstrated; but especially, sufficient stress was not laid upon the distinction between type of organization and grade of development.

Since, in fact, the embryo becomes gradually perfected by progressive histological and morphological differentiation, it must in *this respect* have the more resemblance to less perfect animals the younger it is. Furthermore, the different forms of animals are sometimes more, sometimes less remote from the principal type. The type itself never exists pure, but only under certain modifications. But it seems absolutely necessary that those forms in which animality is most highly developed should be furthest removed from the fundamental type. In all the fundamental types, in fact, if I have discovered the true ones, there exists a symmetrical (*gleichmässige*) distribution of the organic elements. If now predominant central organs arise, especially a central part of the nervous system, according to which we must principally measure the extent of perfection, the

type necessarily becomes considerably modified. The Worms, the Myriapoda, have an evenly annulated body, and are nearer the type than the Butterfly. If then the law be true, that in the course of the development of the individual the principal type appears first, and subsequently its modifications, the young Butterfly must be more similar to the perfect Scolopendra, and even to the perfect Worm, than conversely the young Scolopendra, or the young Worm, to the perfect Butterfly. Now if we leave out of sight the peculiarities of the Worm, the red blood, &c., which it attains at a later period, we may readily say that the Butterfly is at first a Worm. The same thing is obvious in the Vertebrata. Fishes are less distant from the fundamental type than Mammalia, and especially than Man with his great brain. It is therefore very natural that the Mammalian embryo should be more similar to the Fish than the embryo of the Fish to the Mammalian. Now if one sees nothing in the Fish but an imperfectly developed Vertebrate (and that is the baseless assumption to which we referred), the Mammalian must be regarded as a more highly developed Fish; and then it is quite logical to say that the embryo of a vertebrate animal is at first a Fish. Hence it was that I asserted above (§ 1.), that the view of the uniserial progression of animals was necessarily connected with the prevailing idea as to the law of development. But the Fish is not merely an imperfect vertebrate animal; it has besides its proper ichthyic characters, as development clearly shows.

But enough! I have attempted, in embodying the course of development; to show also, that the embryo of Man is unquestionably nearer to the Fish than conversely, since he diverges further from the fundamental type; and upon this ground alone has much been inserted that is problematical, as the umbilical attachment of the Monotremata. In detail, this representation can as little exhibit all the relations justly, as any other representation of organic relations upon a plane surface—even if the investigation were complete, instead of being just begun.

Let us sum up the contents of this section as its conclusion. The development of an individual of a certain animal form is determined by two conditions:—1st, by a progressive development of the animal by increasing histological and mor-

phological differentiation; 2ndly, by the metamorphosis of a more general form into a more special one.

Corollaries to the Fifth Scholium.

The history of development is the true source of light for the investigation of organized bodies. At every step it finds its application, and all the conceptions which we have of the mutual relations of organized bodies must experience the influence of our knowledge of development. It would be an almost endless task to demonstrate this for all branches of investigation. Since, however, those conceptions must spontaneously modify themselves so soon as the course of development is otherwise understood, we may be permitted to bring forward a few points in order to exhibit the influence of the view here set forth, and thereby to justify the length at which it has been given. I have endeavoured also to arrange these additions or appendices, so that those which come first may contribute to the understanding of the subsequent ones; yet I have not been able always to succeed in doing this without intercalating many explanatory episodes. The reader will have also to complain of repetitions. The greatest repetition of all however is, that all these considerations are nothing more than reflexions of the contents of this Scholium.

First Corollary.—*Application of this Scholium to the Doctrine of Arrests of Development.*

It is no longer necessary to demonstrate that monstrous growths can only be understood by knowing the normal course of development. But I may be permitted to say a word concerning arrests of development, since sometimes the understanding of these malformations has been considered to be inseparable from the view of the progression of the higher through the lower forms of animals; and it might thence be believed that a contradiction of the latter view contradicted the doctrine of arrests of development. This doctrine, however, is too well based to be shaken by any alteration in the views which are entertained with regard to the differences of form in the course of the development of the higher organisms. Yet these malformations must not be regarded as the permanent forms of some other

animal which the embryo had to pass through, but simply as a partial stoppage at an earlier stage of their own development. At times unquestionably there exists an obvious similarity with some permanent form in particular parts; but it is as readily demonstrable that this similarity is not the condition of the malformation, but the result of other relations, either,—1st, because that form is nearer the fundamental type, in which case any stoppage at an earlier period of development must necessarily approximate the higher form to it; or, 2ndly, because the altered formative conditions may approximate the formative conditions of the same part in another animal. Thus, for example, the nose in Man is sometimes elongated into a proboscis, which reminds one of the snout of a Pig. But the human nose never passes through any stage of development in which it resembles the snout of a Pig; on the other hand, the Pig's snout, at the fourth week of embryonic life, is not only similar to that of a human embryo at an early period, but is in fact much more like the nose of the adult Man than at a later period.

This relation agrees perfectly with the general law. The nose of air-breathing Mammals in general does not project beyond the jaw. Both the peculiarity of the Pig's snout, therefore, and that of the human nose, arise subsequently without any transition of the one form through the other. If then a Man has the snout of a Pig, it is no arrest of development, but the consequence of an abnormal development, which has a result like that in the Pig, where it is normal. While we are speaking of the abnormal forms of the nose, I will call to mind the "Wolf's jaws," an indubitable arrest of development, but which is certainly no stoppage at any earlier form of animal.

SECOND COROLLARY.—*Application of the present View to the Determination of the separate Organs in the different Forms of Animals.*

A closer acquaintance with the history of development will sooner or later furnish us with the sole safe grounds in the determination of the fitting denominations for, and in forming a just judgment of, the organic parts of the different forms of animals. At present a little may be done in this direction.

Since, in fact, every organ becomes what it is only by the

mode in which it is developed, its true import can only be recognised by knowing the manner in which it is formed. At present we judge for the most part in accordance with an indefinite feeling, instead of considering every organ only as an isolated development of its fundamental organ, and determining from this point of view the agreements and differences among the different types. Every type has, in fact, not only its fundamental organs, but in each these are again divided into special organs, which cannot be exactly what they are in any other type. We therefore need some complete nomenclature, which shall not merely apply the names of organs found in the vertebrate type to the organs of other types, but shall give to them special names when they have a different origin. This requirement will hardly indeed be satisfied in a century, but it is well to call attention to it. In fact, the immediate consideration of the perfect animal has often led to the recognition of the essential difference; perhaps, however, the determining conditions have been less easily comprehensible.

First of all, I would refer to the question how the series of ganglia upon the abdominal side of the Articulata is to be named. They certainly do not constitute a spinal cord, since this is composed of a nervous tube, which can be produced only upon that scheme of development, which is followed in the Vertebrata. As little are they comparable to the sympathetic nerve of the Vertebrata, for they supply voluntary muscles, and in the Articulata the plastic nervous system lies upon the dorsal surface*. They are rather the terminations of the symmetrical nerves of animal life, and, on that very account, as Weber and Treviranus have already remarked, they are comparable to the nerves and ganglia called spinal, in the Vertebrata, on account of their insertion into the spinal cord. In the Articulata, however, these nerves have only one series of central and peripheral

* Some time ago, indeed, I was inclined to consider the so-called recurrent nerves of Articulata to be their plastic nervous system, because I had traced them a long way in the Crab; however, I first became fully instructed on this subject by a letter from Prof. J. Müller. Müller, by his exactness in investigation and delicacy in dissection, has succeeded in following out these nerves through the whole extent of the plastic organs; and he has had the goodness to communicate an excellent drawing of them to me.

ends, because the whole animal part of the body is singly, and not doubly symmetrical.

Whether the anterior pair of ganglia of the Articulata is to be called a brain or not, depends wholly upon the signification given to the word 'brain.' It is assuredly not *the organ* which we call brain among the Vertebrata, for this is the anterior extremity of that nervous tube which is absent in the Invertebrata. It is rather the most anterior pair in the series of ganglia, and since these are to be compared with the spinal ganglia of the Vertebrata, the so-called brain appears to be for the longitudinal type what the Gasserian ganglion is for the Vertebrata. This also receives nerves of sense. A great importance appears to be attached to the circumstance that it lies *above* the œsophagus. This, however, appears to me to be an erroneous view. Properly speaking, it only lies in *front* of the œsophagus.

If, in fact, we form a purely ideal notion of the longitudinal type, the oral aperture is not placed at the anterior extremity, but is directed downward, just as the oral aperture of the Vertebrata is not situated at the anterior extremity of the vertebrate type, but is placed somewhat posteriorly towards the abdominal surface, for which reason a portion of the abdominal visceral plates, the walls of the nose, lie in front of and above the oral aperture. In the Chick it is very clear that the mouth opens below. That in the Articulata the oral aperture belongs to the lower half of the simple ring, is shown very clearly by the Crustacea, and even by forms which exhibit the type in a less altered form, as the Annelida. In the Earthworm, for example, this relation of the so-called proboscis, which extends beyond the oral aperture, is obvious. It contains the most anterior imperfectly developed rings. Now if in the Articulata the oral aperture is in fact anterior, but yet upon the lower surface, and corresponds with the most anterior extremity of the abdominal surface, a pair of nervous ganglia must necessarily lie in front of the oral aperture, and that they lie nearer the upper wall than the posterior ganglia arises partly from the passage of the mouth, partly from the very fact of its occupying the anterior extremity. Very frequently it lies actually in the same plane with the others, as in the Crustacea, where the mouth lies further back; and in Insects, where the head, with the oral aperture, is directed more

or less downwards. Only in the Annelida is its position decidedly, though only a little, superior.—(p. 235.) . . . . .

p. 236. The same holds good of the cervical nervous band in the Mollusca. It is not the organ which we call *brain*, not even in the Cephalopoda, but in a manner the central part of a nervous system, which, in its general relations, may be compared with the plastic nervous system of the Vertebrata, but which takes on a different form, inasmuch as it is not dependent upon a predominant brain and spinal cord. I can regard the so-called brain of the Cephalopoda only as the cervical nervous band of the Gasteropoda. In the former the ganglia are fused together, in the latter they are more distinct. It is a centre of the plastic nervous system, and can only be compared with the ganglia which, in the Vertebrata, give off threads to the organs of the senses and other parts of the head—here, however, possessing no predominating centre, but being subordinate to the brain.

If, in the Vertebrata, we consider the *ganglion maxillare*, which also receives a nerve from the ear, in combination with the *ganglion caroticum*, *petrosum*, *Vidianum*, *ciliare*, and the threads which pass to the organs of sense and the pharyngeal apparatus, we have a similar ring through which the commencement of the digestive canal passes.

That every portion is to be understood only by its relation to the type and by its development out of it, is taught still more strikingly by other parts. The tracheæ of Insects are indeed aëriferous organs, but not the organ which we call the trachea in the Vertebrata, because the latter is a development of the mucous canal, while the tracheæ of Insects arise either by histological differentiation or by involution of the external integument. Sometimes the same name has been used for different organs only from the want of some other word—the difference, however, having been universally recognised. Thus no anatomist has regarded the wings of Insects as of the same nature as the wings of Birds. In the feet, also, the essential differences of the first joints have perhaps never been overlooked. A special name has, with justice, been applied to the antennæ. They have no representative in the Vertebrata. But that they are the wings of the cephalic ring is demonstrated not merely by their position, but by their mode of development. They have

the same relative position as the wings in the pupa, with this difference only, that they come from the head.

For the same reason also they agree with the lateral appendages of the Crustacea. Whatever sensitive properties then these antennæ may have, they are yet never the organs of touch, smell, or hearing of Vertebrata, but sensitive cephalic wings.

By these remarks I wish to render it intelligible, why every type must be studied for itself, and possesses fundamentally peculiar organs which are never to be found exactly the same in any other type. In some cases, indeed, the distinction is but small. The alimentary canal arises in all animals from the surface which is turned towards the yelk. We have here the smallest original difference. But in its further subdivision into organs a distinction must be discoverable for the signification of the separate organs; it is indeed, as we know, often difficult to recognise single divisions, as the stomach, &c. We shall succeed better if we determine every part only after other animals of the same type. We know, for instance, how little the sexual organs of the Massive series can be interpreted by those of the Vertebrata. Still more striking is the tentacular system with its vessels, which is found in manifold variations among the Radiata, for the ciliated bands of the Beroidæ and the circular vessel of some (if not of all) Medusæ, should perhaps be regarded as modifications of this system. In the Articulata and Vertebrata, however, we are acquainted with nothing similar. It is perhaps peculiar to the peripheral type.

It will suffice merely to remark how little the notion that all animals are only detached organs of Man corresponds with nature. A few organs of the Vertebrata may, however, certainly be said to contain within themselves the organs of the Massive and Articulate series; at least this appears to me to be probable with regard to the organs of sense.

I shall perhaps, in another treatise, show that even in the Vertebrata, development alone can guide us in interpreting the signification of the organs.

THIRD COROLLARY.—*Application to the Affinities of Animals.*

I have above ventured to assert (Schol. V. § 1.) that the notion of a uniserial succession of animals is the prevalent one, and I

foresee that this assertion will be regarded as too sweeping, since only a few investigators of the present day declare themselves for it openly and decidedly; in fact, not a few have pronounced decidedly against it. I must therefore devote a few lines to show the correctness of my statement.

That doctrine has, as I believe, far more unconscious than conscious advocates. It seems to me, indeed, that a number of conceptions, proceeding from the uniserial view, and belonging to times long past, have propagated themselves, and without our knowledge have given a colour to our view of organic affinities, which is not the result of investigation. Are not the notions that Cephalopoda or Crustacea are allied to Fishes, or even pass into them, expressions of this fundamental view? They could hardly have proceeded from an immediate and free comparison of their organisms.

Just as incomprehensible is the alliance between Echinoderms and Mollusks.

Do not these attempts to build bridges between two distant countries proceed from the endeavour to make each a link in a chain? Having learnt, in fact, to understand the Crustacea according to the type to which they belong, and regarding them as the most developed forms of this type (with which I do not agree), the next endeavour was to pass from them a step further. In the same manner it was believed that a way led from the highest Radiata to other regions. If, however, in accordance with our view, we regard the separate forms or groups of forms as variations upon a theme, we shall find that the transitions are but few and isolated; consequences of the modifiability of a form, but on that very ground not in themselves necessary and determinate. We shall then not be misled into seeking agreements between things which are heterogeneous, since we do not regard the serial succession as the condition of the varieties of animal forms.

The controversy, whether the Articulata or the Mollusca are the higher, seems to me also to depend upon this view of a uniserial development. If we properly comprehend the essence of the different types, it appears easy enough to comprehend how the plastic formations predominate in the one, in the other sensitive and motor organs. The heart and the liver of Mollusks,

as well as their glandular system in general, then will not necessitate us to place them higher than the Articulata. It would be almost as one-sided to raise all these above the Mollusca, although in general the greater variety in their vital manifestations might give them a fair claim to such a position. Fundamentally, however, each of these sections of the animal kingdom has its own standard, which can only be determined by its type. The greater the histological and morphological differentiation, the higher, according to our view, is the perfection in the same type. A less morphological differentiation is, however, always an approximation to the fundamental type. Thus, the Annelida, on account of the similarity of their limbs, appear to us to be of lower organization, notwithstanding their vascular system, whose limitation in Insects is readily comprehensible, as a consequence of the development of their tracheæ. For us the Myriapoda do not stand much higher, their manducatory instruments being true cephalic feet and their head being but little separated from the other almost identical rings. In the Thysanura and Parasita a greater morphological differentiation has arisen. And the structure of the true Insects is in them, as it were, sketched out.

Just as gradual modifications of the Annulata may be recognized through Myriapoda, Thysanura and Parasita, so may such be observed through the Isopoda, Amphipoda and Stomapoda to the Decapoda, and through the Scorpionidæ to the Arachnida.

For what reason, however, the proper Spiders, or the Decapoda among the Crustacea, are to be reckoned as more perfect than the true Insects, is not clear. On account of their more perfect vascular system? This is only a consequence of a less active interchange with the air, whose more powerful influence always assists the development of animal life.

If, on the other hand, the Individualization of the organic constituents is to be our standard of perfection, we observe in the Decapoda, besides the slight histological differentiation which to me is obvious, a tendency to compress the organs of sense, the motor and the plastic organs, into one chief centre,—in consequence of which the type is greatly modified, but its essential parts become little separated; in the Arachnida the plastic body

is at least separated from the animal; but in Insects with metamorphosis, sensibility, irritability and plasticity are separated, though indeed only in the perfect state. The most highly developed among these, again, appear to me to be those whose thoracic segments are not divided into many separate rings, as in the Flea, the Coleoptera, and the Orthoptera, but when they are collected into one. It is in these that the originally similar parts, such as the feet and manducatory organs, have attained the widest deviation. It is in these that we meet with the best developed wings and the most various manifestations of life. The Crustācea, indeed, possess an ear and a nose; but we must not forget that the head of Insects is small enough to make such organs doubtful; that a few investigators believe they have found them, and that, at any rate, the senses are not absent.

If we have succeeded in getting rid of all preconceived notions of a gradual series, we shall consider each form to be a modification of a more general form, and that these are modifications of a fundamental type, and learn to comprehend them from this point of view. We shall then take more pains to determine the general affinities of each species, than its place in a universal progressive series.

If we seek, however, for the grade of development, we must look for it only according to the degree of differentiation of the parts, and within the type which belongs to the animal. That, however, in fact, the preconceived conceptions of a progressive series have led to the ordinary views, is what I shall endeavour to establish and explain by yet a few examples.

We often hear of retrogressive metamorphoses of a whole animal form or of a single organ;—can any clear conception attach to these "Retrogressions," if we do not assume that the form of some one animal is the condition of the form of some other? This much, however, is certain, that such a view implies the conception of a serial progression.

If, in fact, we arrange together obviously allied animals, and then place them with their highest forms below those of another series, we shall have a retrogression. I will but shortly refer to the above (Schol. V. § 3 *a*) example of Fishes.

In truth, the retrogressive metamorphosis of particular organs

is spoken of, under the supposition that there is a progressive development for every organ, from the Monad to Man, and that this development is realized in accordance with the order of progression of the animals, the particular exceptions from which are now given. If, however, the organs are modifications of fundamental organs, and these differ according to the scheme of development (compare the following Corollary), there would appear to be an erroneous assumption in this very supposition. I believe, therefore, that if comparative anatomy is to be directed to the ascertainment of the laws of formation, the only proper way is, besides the constant reference to a fundamental type to which the whole animal belongs, to compare the organs by themselves in their different forms, as Burdach has attempted to do in his 'Physiology,' without arranging the forms in the same order as the animals to which they belong would take in accordance with their perfection in other respects. We shall thus perceive how the general structure of the whole body of an animal, or its relation to the external world, operates in modifying the form of particular organs, and so prevent ourselves from being misled by prejudices.

That, however, these retrogressions in the development of organs are only an appearance which depends upon a presupposed uniserial development, is rendered most obvious by their disappearance, if we arrange the animals according to another organic system than that which was previously used as a base. I bring forward one example out of many. If I am persuaded that the Articulata are to be arranged in a progressively developed series, and dispose them according to the development of the vascular system, I may order them thus: True Insects, Myriapoda, Arachnida, Annelida. In this case the eyes are retrogressive through the series. Of the respiratory organs, and the vascular system besides, it is at once intelligible that the one appears retrogressive with respect to the other, since these systems are antagonistically related. If I consider them as modifications of a fundamental type, in which sometimes one and sometimes the other system is more changed from the simple fundamental form, then all retrogressions disappear.

What I have here said of the Articulata, in order to select an obvious example, holds good not of them alone, nor merely of

the antagonistic relation of respiratory organs and vascular system;—it appears wherever there are any manifold variations. If we regard the different forms of Mammalia, we find for one series of organs other affinities than for another. If we consider the development of the animal part, which we may most readily estimate by the skeleton, the Bats are very different indeed from all the proper quadrupeds. We must suppose that they form the most aberrant order. With respect to their digestive organs, they resemble the Insectivora. Pallas, who in the *Zoographia Rosso-Asiatica* unites the Bats closely with the Mole, appears therefore to me to be as fully justified as Tiedemann, who about the same time, in his 'Zoology,' separated them widely. For the same reasons, Tiedemann unites the Seal with the Dugong, while by Pallas they are widely separated. The one has regarded the extremities, the other the teeth. What do such facts prove, except that the different organic systems vary in different modes? The Mole and the Bat seek the same prey, the one in the air, the other in the earth. Their motor organs therefore differ according to the place of their residence. The Dugong and the Seal are both aquatic, and have fin-like extremities, but what they seek is totally different; so are their dentition and their stomachs.

Under such circumstances, does not an approximation to Man give for every organic system a different series of animals; and if this be so, are not "retrogressions" without meaning? In truth, Man is only in respect of his nervous system, and of that which is connected with it, the highest form of animal. His erect progression is only a consequence of the greater development of his brain, since we find everywhere that the more the brain preponderates over the spinal cord, the more it raises itself above it. If this remark be well founded, all corporeal distinctions between Man and other animals may be reduced to cerebral development; and in that case the pre-eminence of man is only a partial, although the most important one. One must be completely prejudiced, in fact, not to see that the stomach of the Ruminant, which changes grass into chyle, is more perfect than the stomach of Man.—(p. 242.)

(p. 257.) FOURTH COROLLARY.

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But from what has been said, it seems to follow that every principal type of animal organization follows a special scheme of development; indeed nothing else could have been expected, since the mode in which the parts are united together can only be the result of the mode of development. In reality, therefore, I might have used, instead of Type and Scheme, a common term expressing both. I have only kept them separate in order so to make it obvious, that every organic form, as regards its type, *becomes* by the mode of its formation that which it eventually *is*. The scheme of development is nothing but the becoming type, and the type is the result of the scheme of formation. For that reason the type can only be wholly understood by learning the mode of its development. This introduces differences into the germs, which at first are alike in all essential points. Different conditions or formative powers must act upon the germ in order to produce this multiplicity, on which head we shall by and by raise one or two queries.

Here, however, we must add the remark, that the original agreement of all animal germs does not completely disappear even in the perfect forms, and that we have to seek the most profound distinctions among animal forms, which are attainable by us in the mode of development.

With respect to the original agreement, I would call to mind, that, according to the Corollary of the Second Scholium, every animal is at first a part of its mother, that it becomes independent either by the immediate development of the parent herself, or after the action of a male principle, and that then the first act of independence consists in passing into a vesicular form; either the whole becoming the body of the new animal, or the future body (the germ) separating itself from the merely nutritive substance which surrounds it. Here animals and plants diverge, since the latter do not invest the nutritive matter. The vesicular form, therefore, is the most general character of the animal; the contrast of external and internal surface is the most general, and therefore the most essential contrast in the animal. (See above, Schol. V. § 4 *d*.)

There remains yet another agreement between all forms of development. In all animals, namely, which at an early period possess a germ and a yelk, the investing germ becomes divided into many layers; that turned towards the yelk is the plastic receptive layer; that turned from it, the more animal, even though its outermost border should become merely a limiting organ, and clothe itself more or less with an excreted non-vital layer. That now the vascular system, if it is otherwise separated from the digestive cavity, is formed external to it nearer to the animal part; that in the animal part, muscles, nerves, &c., become separated, appears also to belong to the Idea of the animal in general; and the further this histological differentiation goes, the more developed do we call an animal.

Wholly different from this, however, is the relative position of the parts. This is determined by the external form of the development.

We have distinguished four principal forms, or, as we have called them, Schemata of Development:—

Radiate Development (*Evolutio radiata*), which, proceeding from a centre, repeats similar parts peripherally.

Coiled Development (*Evolutio contorta*), in which similar parts are twisted round a cone or other space.

Symmetrical Development (*Evolutio gemina*), in which similar parts are distributed from an axis on both sides to a sutural line opposite to the axis.

Double Symmetrical Development (*Evolutio bigemina*), in which from an axis similar parts are disposed on both sides above and below, and are united at two sutural lines; so that the inner layer of the germ is closed below and the upper layer above.

We know that in the higher Vertebrata the Germ soon divides into two parts,—an inner, which may especially be termed the Embryo; and an outer, which may be called the Germinal membrane. I have already remarked that the former is nothing but a part of the germ, which is metamorphosed according to the scheme of development peculiar to every animal, whilst the peripheral part remains behind in its development.

In Mammalia, Birds, and Reptiles, the middle part is but small in proportion to the outer portion, and it gradually sur-

rounds the yelk, forming the abdominal suture. In the Frog, indeed, the external part of the germ is very thick, yet, as I believe, a separation into embryo and germinal membrane is undeniable; for the middle portion at the period in which the back closes is still very much thicker, and the limitation is tolerably well marked between the abdominal plates and that exterior portion which I regard as the germinal membrane. The former grow together towards the suture of the abdomen. In very young Pikes, also, in which the germinal membrane is much thinner and more transparent, this appeared to me to be the case. I saw beside the trunk of the vertebral column a pair of very narrow dark striæ, the commencing abdominal plates. It may hence, I believe, be affirmed universally of the Vertebrata, that the embryo will surround the yelk with its abdominal plates, although this has previously been invested by the germinal membrane. It is the same in the Articulata. Their lateral plates are clearly distinguished by their thickness from the proper germinal membrane. They also surround the yelk. In the Mollusks, however, the whole germ appears to change equally. It cannot therefore be said of them that the embryo grows round the yelk, but more justly, that from the moment of fecundation it *remains* as its investment; for a differentiation of the germ into embryo and germinal membrane is not perceptible; the whole germ, rather, becomes the embryo.

The same would very probably also take place in the radiate type, if any animal form from this series were developed from a true ovum, of which we have no knowledge*. If they should all be developed from mere germ-granules, the relation is still more apparent; for every germ-granule, so far as we know, is developed as a whole, and is nothing but a germ without a yelk.

We must not overlook here an interesting relation. In those ova in which the germ is clearly separated into an embryo and a germinal membrane, it is the animal part of the embryo which

* At present hardly anything could be of more interest for the history of development than the observation of the development of the Asteridæ, and after these of the Cephalopoda. According to Cavolini, the latter have a yelk-sac depending from the mouth (*Abhandl. über die Erzeugung d. Fische und Krebse uebers. von Zimmermann*, 1792, p. 54), which is difficult to understand.

causes this separation. It is the animal part which grows so much, that we observe the marking off of the embryo from the germinal membrane. It is only after this has determined the whole form of the animal, that the plastic part appears to attain a certain degree of independence, which in the Articulata is often limited to a mere separation, the separate organs arising subsequently, but which in the Vertebrata has sufficient power to cause a symmetrical development of the animal part. Of the action of the plastic part upon the animal, we can but detect a trace here and there. It is otherwise in the Mollusca. The plastic part becomes independent very soon, and has a decided influence upon the external form. We see how the essential character of the animal manifests itself very early, and development affords a justification for the name of Plastic animals which has been given to the Mollusca. Hence also we shall be better able to judge how far the Mollusca may be justly compared with the vegetative section of the body of the Vertebrata; in its predominant character namely, not according to the sum of all its separate parts. In the Mollusca, it is also a relatively animal part which occupies the whole periphery, and is principally developed in the foot of the Gasteropoda. Compared with other animals, they are living bellies; but since these bellies are independently developed, without the influence of a more highly organized animal part, they have also a part which for them is more animal, and it is that which originally formed that surface of their germ which was turned from the yelk.

In all four forms the surface of the germ which is turned towards the yelk does not change its position relatively to the latter, but retains it, and becomes the digestive surface of the perfect animal. In all forms, moreover, the peripheral part of the perfect animal is the external surface of the germ, that which is turned away from the yelk. I therefore believed myself to be justified in supposing that it is the relation to the yelk which in the germ produces the primary differentiation into an animal and a plastic layer.

But it is not in all animals that the *whole* outer layer of the germ remains exterior. In the Vertebrata, the one half of the doubly symmetrical development encloses a part of the outermost surface, and changes into the nervous tube, the spinal cord with

the brain, parts which must therefore necessarily be absent in other types. I would here render perfectly obvious how it is the scheme of development which produces the principal character of the animal. If we suppose that, in any articulate animal which is in the earliest stage of its development, a part of the germ should become raised up on both sides, and so enclose a portion of the external surface, the enclosed part would be an animal central portion. The internal organs would all have the same relation to it as in the Vertebrata, excepting the plastic nerves, which by the influence of the animal nervous system appear to be approximated to this last in the Vertebrata.

In relation to the external world, however, all the internal organs would be inverted, since the central part itself would lie downwards. If we were to invert the animal, all the outer parts, the extremities and the organs of sense, would be displaced; and supposing that the extensor and flexor sides had not undergone inversion by the addition of the new central part, these also.

Hence we conclude, that, by the origin of a central part for the animal body, the position of the plastic organs, and their relation to the nearest animal layer, have indeed remained unchanged; but their relation to the external world, and all which represents this relation in the body, has become inverted. In the former case, where the course of development is simply symmetrical, the central line from which it proceeds becomes the flexor side of the animal; with a doubly symmetrical development, the side from which it proceeds becomes the extensor side. Towards the flexor side, the extremities and the feet are developed. By this it shows itself to be that which is most essentially turned towards the planet. Towards the extensor side, that turned from the ground, the organs of the senses are developed.

I commenced this Corollary with the remark, that animals ought to be divided according to their mode of development, and I have shown sufficiently at length that the principal types have their own form of development. I may be permitted to point out here, in a few words, that the safest guide for further division would be found in the history of development, if we were acquainted with it with sufficient exactness, in the different

classes and families of animals. If we keep this in view, we shall easily recognise the true Insects as a higher stage of development than the Arachnida and Crustacea. We shall hold the Batrachia to be different enough to separate them, with De Blainville, from the Reptilia as a distinct class. And, in fact, what have they in common with the latter, than that they are not Fish, nor Birds, nor Mammals?

Scholium VI.—*General Result.*

If we review the contents of all the Scholia, a universal result proceeds from them. We found that the action of reproduction consists in elevating a Part into a Whole (Schol. II.): that, in the course of development, its independence in relation to that which is around it increases (Schol. II.), as well as the determinateness of its form (Schol. I.): that in the internal development, the more special parts are developed from the more general, and their speciality increases (Schol. III.): that the individual, as the possessor of a determinate organic form, gradually passes from the more general form into the more special (Schol. V.); and therefore the most general result of these investigations and considerations may well be thus expressed:—

The history of the development of the individual is the history of its increasing individuality in all respects.

This general result is indeed so simple, that it would seem to need no demonstration, but to be cognizable *à priori*. But we believe that this simplicity is only the stamp and evidence of its truth. If the nature of the history of development had been from the first so recognized as we have just expressed it, it would and must have been a deduction thence, that the individual of any particular animal form attains it by passing from the more general into the special form. But experience everywhere teaches that deductions become much more certain if their results are previously made out by observation. Man must have received a greater spiritual endowment than he actually possesses for it to be otherwise.

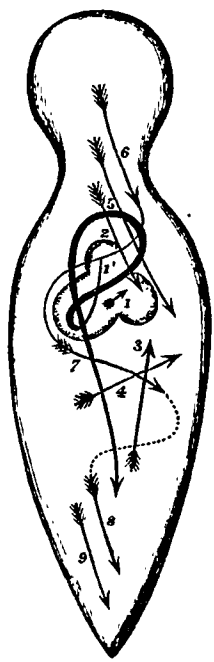
If, however, the general result which has just been expressed be well based and true, then there is *one* fundamental thought which runs through all forms and grades of animal development,

and regulates all their peculiar relations. It is the same thought which collected the masses scattered through space into spheres, and united them into systems of suns; it is that which called forth into living forms the dust weathered from the surface of the metallic planet. But this thought is nothing less than Life itself, and the words and syllables in which it is expressed are the multitudinous forms of the Living.

DESCRIPTION OF FIGURE.

Ideal figure of the organic movements in Vertebrata. The body of the animal is supposed to be transparent, so that the outline only is seen. The outline of the heart is indicated (the right auricle is drawn rather too much backwards). The view is from the dorsal surface.

1'. Course of the red blood into the left ventricle.
1. Course of it out of the left ventricle.
2. Course of the venous blood from the anterior half of the body into the right auricle.
3. Course of the venous blood from the posterior half of the body into the right auricle.
4. Course of the portal blood.
5. Course of the respired air.
6. Course of the food from the pharynx into the œsophagus.
7. Course of the chyme from the stomach into the intestine.
8. Course of the fæces.
9. Course of the ova.



[T. H. H.]

ARTICLE VIII.

On the Development of Zostera. By W. HOFMEISTER.

[From the *Botanische Zeitung*, Feb. 13th & 20th, 1852.]

THE peculiar physiological phænomena exhibited by *Zostera*, above all the unique formation of the pollen and the strange structure of the embryo, have frequently and from an early period drawn the attention of botanists to this remarkable genus of plants. In most of the larger illustrated works devoted to the local floras of Europe, the figures of *Zostera* are accompanied by careful and more or less accurate microscopic dissections, as in Schkuhr, Hooker's *Flora Londinensis*, Reichenbach's *Icones*, Schnizlein's *Iconographie der natürlichen Familien*, &c. The form of the embryo has been a subject of discussion for almost every author who has studied the comparative import of the parts of the seedling plants of Monocotyledons*. Fritzsche† made known the curious condition and the circulation of the contents of the pollen-cells; Grönland‡ has very recently published a contribution to the knowledge of *Zostera marina*,—a series of most acceptable microscopic researches on the developmental history: imperfect, however, in reference to several of the most interesting questions, especially to those connected with the origin of the pollen and of the embryo. The following essay, the materials for which I owe to the kindness of Prof. Nolte of Kiel§, will in some points complete, in others correct, the paper published by Grönland.

The inflorescence of *Zostera*, like that of the nearly allied Potameæ, is relatively terminal: the metamorphosed end of a

* Gärtner, *De Fructibus*, t. 19; Bernhardi, *Linnæa*, Bd. vii.; Jussieu, *Annales des Sc. nat.* 2me Sér. t. xi. p. 356.

† *Mém. de l'Acad. de St. Pétersbourg par div. Sav.* t. iii. p. 703. pl. 3.

‡ *Bot. Zeitung*, vol. ix. p. 183 (1851).

§ The plants which Prof. Nolte was kind enough to forward to me repeatedly, at different seasons, were perfectly fresh when they arrived at Leipsic (30 or 40 hours after their removal from their native locality); even the adherent *Chætomorphæ* and *Polysiphoniæ* retained their vitality unaffected.

branch. In *Zostera marina*, when the formation of flowers commences, both the previously inert axillary buds and also the terminal shoot of the little-branched or even simple sterile plants, become converted into inflorescences. In *Zostera minor* the rule is for axillary sprouts standing far back from the sterile terminal shoot, to become transformed into blossoms. This distinction between the two species, so striking at first sight, appears to depend principally upon the fact that in *Zostera marina* the old portions of the stem die away rapidly, within a few months, from behind forwards, while in *Zostera minor* they persist for more than a year.

When the terminal bud of a plant of *Zostera marina* enters upon a transformation into a spadix, the ordinary series of linear stem-leaves with sheathing bases (having the divergence $\frac{1}{2}$), becomes interrupted by a cylindrical leaf-sheath, devoid of any indication of a lamina, the two lateral borders of which sheath, enclosing the terminal bud, adhere firmly together. The axillary sprouts which become blossoms arise with a similar sheath. The next internode of the flowering sprout bears a leaf like the stem-leaves (*laub-blätter*), but with a comparatively shorter lamina, which, like the leaves of the *Zosteræ* generally, has a divergence of $\frac{1}{2}$ from the leaf next older than itself. The sheathing base of this leaf envelopes the inflorescence, *i. e.* the expanded, flat, long-protracted end of the stem, that surface of which turned away from the last leaf bears the anthers and ovaries.

From the axil of the sheathing bract (*vorblatt*) of the fertile sprout (Pl. VI. fig. 1 *a*) arises a shoot, resembling in all respects its parent sprout, with which it is coalescent for a considerable distance (fig. 1 *b*). At the place where the cohesion ceases the new sprout bears its first, sheathing leaf (fig. 1 b^1). This diverges $\frac{1}{2}$ of the circumference of the stem from the bract (*vorblatt*) of the sprout of the preceding rank, and is parallel with the stem-leaf (*laub-blatt*) in the axil of which that arises. The sheathing leaf is succeeded by a stem-leaf (*laub-blatt*) (fig. 1 b^2), above which the sprout terminates with the inflorescence (fig. 1 *b*). The axil of its lowest, sheathing leaf sends out a fructifying branch of a new rank (fig. 1 *c*), and so on, till the exhaustion of the growing power of the blossoming plant, in

Zostera marina, to a series of twelve, in *Zostera minor* only of six ranks.

The rudiments of the first spadix of *Zostera marina* appear at the beginning of spring, those of *Zostera minor* in the middle of summer. From then until the period of maturation of the first seeds (in *Z. marina* at the beginning of July, in *Z. minor* the beginning of September), new flowering sprouts arise successively in the axils of the bracts (*vorblatter*) of their predecessors, so that, from the middle of May forwards, every fertile plant of the common *Zostera* exhibits a series of distantly situated stages of development of the floral organs*.

When arising out of the axil of the sheathing leaf of the preceding sprout, the axis of a new rank, terminating in an inflorescence, presents itself as a hemispherical papilla (fig. 1 *d*), the side of which facing the parent sprout coheres with the latter up to the point where the new shoot forms its first, sheathing leaf, by the simultaneous multiplication of a zone of cells situated close underneath its apex. The multiplication of the cells of both organs, axis as well as leaf, in the longitudinal direction, commences with a repeated subdivision of their apical cells—in the axis of a single one, in the leaf of an incomplete crown of similar cells—by means of alternately obliquely inclined walls.

The fertile shoot forms its single stem-leaf (*laub-blatt*), opposite to the leaf-sheath, shortly after the latter breaks forth. The bud of the sprout of the succeeding rank appears simultaneously in the axil of the basilar sheath.

The stem-leaf (*laub-blatt*) makes its appearance as a flat cellular mass embracing the end of the stem so completely as to leave only a narrow slit. It first grows longitudinally, by re-

* The interpretation of the series of sprouts of the flowering *Zostera* given above, placed beyond doubt by investigation of the development, is also the only one possible, looking exclusively at the condition when complete. Neither is the supposition admissible that the flowering sprouts, upwards from the sheathing leaf, are a series of equivalent secondary axes of a main axis bearing only sheathing leaves, for the sheath is opposite to the sprout terminating as an inflorescence;—nor is that which would make the inflorescence an axillary bud of the stem-leaf (*laub-blatt*) which sheathes the spadix with its base, for this assumption would lead us to expect each couple of leaves of the main axis, a stem-leaf (*laub-blatt*) and a leaf-sheath, to stand regularly one above the other; a conception untenable when we recollect the $\frac{1}{2}$ position of the leaves of the sterile plant of *Zostera*.

peated subdivision of the cells of its upper border. The multiplication of these cells, on the side turned away from the slit, of this organ (hitherto resembling a cylinder slit up lengthways), soon outstrips that of the apical cells of the other half of the leaf: the riband-shaped lamina grows out from the sheath. The multiplication of the cells at the apex of the leaf ceases early, while a very active and long persistent increase occurs in those of the base.

After the rudiment of the stem-leaf (*laub-blatt*) has been formed, the end of the stem above it changes its form. It becomes widened out by a multiplication of its cells, predominantly in the direction parallel to the surface of the leaf, and it assumes the shape of a thick spatula, slightly concave at the side nearest the next (younger) sprout. The rudiment of the flattened spadix is now unmistakeable in the end of the axis. The longitudinal growth of the spadix is continued by a frequently repeated division of its apical cells by means of walls inclined alternately towards the upper and lower surfaces of the leaf-like organ. The cells in the median line and at the margins of the spadix remain long capable of multiplication; constituting strings of cambium structure. On the other hand, two broad strips of cellular tissue, parallel to the lateral borders of the spadix, early cease to increase. With the exception of those composing the epidermis, all these cells become separated from each other at their angles; air becomes excreted in the intercellular spaces (fig. 3). The cells of both the marginal strips of cambium on the upper side of the spadix become greatly multiplied through repeated division by walls parallel to its surface. In this way are formed two swollen tracts of cellular tissue, which, in their further development, become curved strongly inwards so as to cover in a great part of the upper surface of the spadix, through the resistance which the sheath of the stem-leaf (*laub-blatt*), closely enveloping the inflorescence, opposes to the unfolding of them. In *Zostera minor* little leaf-like structures arise upon the spadix near the lateral margins of its upper face, and these lie over the surface of the spadix like clamps or claws. *Zostera marina* exhibits no trace of such organs. From the median streak of the spadix, which becomes greatly expanded by the active multiplication of its cells, arise the anthers and ovaries, upon the upper face,

arranged with strict regularity, as is well known, according to $2\frac{1}{2}$, in such a manner that single anthers alternate with single ovaries in each of the two longitudinal rows of floral organs, and organs of different sex constantly stand next together horizontally.

The anther first appears as a longish papilla of cellular tissue, the larger diameter of which is parallel to the longitudinal line of the spadix (fig. 4 *a*). The two ends of the young anther soon appear curved outward to some extent; they rapidly increase in magnitude, and become globular protuberances (fig. 3 *a*, *a*), which gradually become spindle-shaped through continued rapid multiplication of the cells. Thus each anther consists of two apparently independent, moderate-sized halves, which are connected together by a comparatively long riband-shaped cellular body, the altered connective, attached to the spadix by the narrow edge*.

At the time when the half of the anther is passing from the globular into the ovate form, two parallel rows of cells lying in its longitudinal axis, take on a different character from the surrounding tissue (Pl. VI. figs. 5–7). The process of division ceases in the former, while the three layers of cells of the latter continue to multiply. The cells of these parallel rows are the primary parent-cells of the pollen. Their form is pretty nearly that of a cube (fig. 7); in their subsequent development they become elongated into short prisms, in a direction inclined downwards from the surface of the spadix.

The pollen-cells are developed from these cells through repeated longitudinal division, by means partly of perpendicular, partly of horizontal walls (figs. 6–12). The process of their formation is thus very unlike that occurring in the great majority of Phanerogamia. There is not the slightest indication of parent-cells becoming isolated, or of special parent-cells. There occurs in the primary parent-cells a series of "halvings" or bisections in only two directions, differing in no respect from vegetative cell-multiplication; the last generation, alone, of the daughter-cells become disconnected and so form the pollen-cells. This development of the pollen of *Zostera*

* This part of the development of the anther, very completely treated and correctly figured by Grönland, *loc. cit.* 187, is mentioned here merely for the sake of giving a connected account.

is not, however, altogether an isolated phænomenon; the earlier stages of formation of the pollen-masses of the Asclepiadaceæ resemble it most perfectly. In the anther of the Asclepiadaceæ, the laws of growth of which correspond on the whole to those of the rudimentary spadix of *Zostera*,—and which, like this, is at an early age shaped like a little sloped-off spatula with a strongly rounded back,—two groups of longitudinal rows of cells become the primary parent-cells of the pollen*. Extending considerably inwards in a direction perpendicular to the surfaces of the anthers, they acquire a different character from the surrounding tissue and assume the form of recumbent prisms. By a series of longitudinal and transverse divisions parallel to the long axes of these prisms, the rudiment of the pollen-mass becomes a group of narrow cells of a length six to ten times greater than the cross diameter. At this stage of development it corresponds perfectly to the contents of a chamber of the young anther of *Zostera*. But in the Asclepiadaceæ there now succeeds a many times repeated division of the elongated parent-cells, by means of walls perpendicular to their long axes, whereby the pollen-mass becomes transformed into a body composed of transverse rows of cubical cells—the special-parent-cells. These special-parent-cells become polyhedral by unequal expansion of the whole mass, and then a pollen-cell originates in each.

The pollen-cell of *Zostera* appears at its origin as an obtuse-angled, almost cylindrical sac, the long diameter of which is three or at most four times as great as the cross diameter (figs. 11–13). The nucleus, which it is difficult to make visible, vanishes at an early period.

With the formation of the pollen commences a very considerable enlargement of the pollen-chambers (loculi), by vigorous multiplication and expansion, in a tangental direction, of their

* Schacht (*Das Mikroskop*, Berlin 1851, p. 154) assumes that only one longitudinal row of cells becomes converted into primary parent-cells. His figure (tab. iii. fig. 8) shows the cross section of the attenuated upper end of an already further developed group of such cells (a pollen-mass), where one primary parent-cell, divided into two, is visible. Longitudinal and transverse sections of earlier conditions show, beyond doubt, that *several* longitudinal rows of cells of the tissue of the rudimentary anther, of unlike value (in Nägeli's sense, *i. e.* not all products of an equal number of subdivisions), take part in the formation of the pollen. I shall recur to this subject in another place.

cell-walls. The pollen-cells, constantly growing longer, keep pace with the enlargement of the loculi; they thus soon attain a considerable (fig. 14), and finally, in proportion to the permanently small cross diameter, quite an enormous length (in the ripe anther as much as 3 lines). They retain throughout their original direction, inclined downwards from the surface of the spadix. Toward the close of the increase of length they displace the innermost of the three layers of cells which originally formed the outer wall of each *loculus*. A cellulose membrane becomes first distinguishable on the pollen when the long diameter is about eight times the cross diameter, and at that period it is yet extremely delicate. As the pollen approaches maturity it becomes tougher, but no secretion whatever of an *exine* occurs; as was made known by Fritzsche. The tendency of the pollen-cell to expand its membrane often outruns the growth of the walls of the loculus, towards the approach of maturity. The pollen-cells, restrained in their natural extension, then frequently exhibit curvatures or curling of the ends and protrusions of various forms (Pl. VI. fig. 15 *b*).

As long as the longitudinal growth of the pollen lasts, the granular-mucilaginous fluid contents are uniformly diffused in the cell. Toward the time of maturity we find longish cavities in the mucilage, filled with a fluid of less refractive power, and these are finally blended into a single cavity lying in the axis. At this period we may frequently observe the active currents in the dense, mucilaginous coating (containing numerous granules) of the inside of the cell-wall; more distinctly in proportion as the pollen-cell is riper and the temperature of the surrounding water higher. Two principal currents may be distinguished, one ascending, the other descending; one of these is ordinarily stronger and of larger size. The moving mass splits up here and there into several arms, sometimes becoming again confluent, between which remain isolated spaces occupied by motionless and more transparent fluid (fig. 15.) The pollen-cells in which a particularly rapid circulation occurs are always greatly swollen up (lying in fresh water), and ordinarily burst in the course of a few minutes during the observation. Change of temperature in the surrounding medium has a most decided influence on the circulation in the pollen-cell. When warmer or cooler water is applied upon the object-holder, one of the two currents is

greatly strengthened, the other weakened, sometimes even so far as to disappear. It is not improbable that the different temperatures of the ends of the filiform cell form one of the causes on which the phænomena of motion of the granular mucilage are dependent.

The investigation of the development of the pollen of *Zostera* is very difficult. The contents of the cells of the young anther, especially those of parent-cells of the pollen-cells, and of the latter themselves, are extremely sensitive to the action of pure water. This holds in a still higher degree of the pellicle forming the coat of the young pollen. When an available preparation, a very delicate longitudinal section of a young half-anther, is placed under water, the membranes of the young pollen-cells swell up, and, with their mucilaginous contents, instantly run together into a shapeless jelly. The only method of examining the young anther is to place it in a saline solution; I employed here, as in similar cases, a saturated solution of carbonate of ammonia. No safe conclusions can be obtained regarding the structure of the anther, or the course of development of the pollen, without making sections. The connection of the different tissues is so intimate in the young anther, that it is quite impossible to extract uninjured either the parent-cells of the pollen or the very young pollen-cells*.

The first visible rudiment of the ovary is a flat papilla (fig. 3 *b*), composed of few cells, which, increasing in size, soon acquires the form of a horse-shoe with the convex side turned towards the median line of the inflorescence (fig. 4 *b*), the rudiment of a leaf attached upon the surface of the spadix. In a short time, this becomes closed in so as to form an annular wall of cellular tissue, within which appears a little roundish mass of cellular tissue (fig. 16 *a*), approached near to the inner border; this is the axillary bud of the carpel—the ovule. The circular wall becomes developed particularly quickly on the side next the base of the spadix. It bulges out at this place, while it grows

* The globular cells which Grönland mentions as the contents of the loculi of the young anthers, and likewise figures (*loc. cit.* p. 188, figs. 18, 19, 20), I was unable to find, at any stage of development of the anther. The closely packed, straight and parallel pollen-cells always completely filled up the cavity of the anther. Probably those appearances depended on some of the cells of the lax and mucilaginous innermost layer of the wall of the anther being accidentally detached in the preparation of the object.

up into an obtusely conical hollow mass of cells perforated at the apex (fig. 17). The ovule unfolds itself within the bulging portion of the cavity, becoming curved downward. Simultaneously with the sudden commencement of the very considerable elongation of the perforated mouth of the young ovary, to form the canal of the style, begins the formation of the two integuments (fig. 18). They arise close beneath the summit of the young ovule, by a pretty nearly simultaneous commencement of rapid multiplication in two zones of cells; the development of the outer coat of the ovule begins immediately after the inner coat becomes visible. The lower part of the ovule, at this epoch by far the larger, remains uncovered by the integuments.

Both integuments grow longitudinally by constantly repeated division of the crowns of cells at their summits, by walls alternately inclined to and from the nucleus (fig. 19). The outer integument soon acquires considerable thickness through two or three repetitions of the division of the cells of the second degree, by means of walls parallel to the free outer surface; when the ovule is fully developed, this coat is composed of lax tissue, traversed by intercellular spaces full of air, enclosed by an epithelium formed of cells one-fourth the size and filled with watery fluid. The cells of the second degree of the inner integument, do not become multiplied in the direction of the breadth until this coat has grown up beyond the summit of the nucleus. Then, however, its upper margin rapidly becomes broader and thicker through repeated division of the cells by means of walls parallel to the long axis of the ovule; the mouth closes in, leaving only the narrow canal of the micropyle (Pl. VII. fig. 22) formed solely by the inner integument; the outer coat of the ovule, which comes to a standstill when the inner begins to increase in size, becomes grown over by the thickened margin of the micropyle.

At the epoch when the integuments reach the level of the summit of the nucleus, the latter is composed of an axial row consisting of a few, eight to ten cells, enclosed by a double layer of cells. A simple layer of cells covers the upper extremity of the axial string and forms the summit of the nucleus (fig. 19). As in most young organs of vegetables, the cells forming the free outer wall of its surface possess tolerable firmness, different from the gelatinous consistence of the cell-walls in the interior.

The uppermost three cells of the row occupying the longitudinal axis of the ovule are distinguishable from their neighbours, at a very early period, by a larger size and greater concentration of their contents; this is particularly the case with the uppermost of them, which gradually grows up to be the embryo-sac, while the nucleus undergoes a profound change of structure by an active multiplication of the cells, especially of those at its lower part.

The cells of the surface of the upper end of the nucleus are divided by longitudinal and transverse septa perpendicular to the outer walls; the same division is repeated in the "daughter-cells." The increase of this cellular hood, in length and compass, thus keeps pace at first with that of the cell growing into an embryo-sac (fig. 20), enclosed by it. A little later begins a very rapid multiplication of the cells of the lower part of the nucleus, in all three directions. In the first place the axial cells divide by perpendicular longitudinal walls; the newly-formed cells again divide by longitudinal walls standing at right angles to those last produced. Thus from this time the embryo-sac no longer rests upon a simple row of cells, forming the axis of the mass of cells below it, but on a column formed of double pairs of cells, which cells become repeatedly divided by horizontal walls (fig. 21). The multiplication of the cells of the two peripherical layers of the nucleus, only weak just below the growing embryo-sac, becomes greater proceeding towards the base, where the hitherto cylindrical mass of cells soon becomes strongly bulged out. The multiplication of cells still continues in this region even after the ovule has attained its normal size, so that at the epoch of fertilization this part of the nucleus is composed of cells one-fourth the size of those lying close beneath the embryo-sac. Finally, the cells of the periphery of the nucleus all divide once oftener by longitudinal and transverse walls than those in contact with them; they thus appear one-half the height and breadth of the latter.

During the further increase of size of the embryo-sac, the cells surrounding it become gradually broken down and compressed. The firmer, free, outer walls of the superficial cells are not attacked by this softening and solution of the cellulose; after the breaking down of the inner tissue has advanced to a certain point, these outer walls of the superficial cells form a homogeneous, connected

membrane, transparent as glass, which encloses, as a sac, the semi-fluid mass of primordial utricles set free by the solution of the cell-coats (fig. 21). The large primordial cell in the centre of this mucilaginous mass, the nascent embryo-sac, from this period begins rapidly to displace the rest, which become by degrees completely dissolved; first of all those bounding it laterally, while the cap of cells covering its summit persists for a short time longer (fig. 21). The primary nucleus of the embryo-sac is always still distinctly perceptible in its centre; radiating threads of granular mucilage pass out from it. Three newly-formed, closely-crowded, globular cells show themselves in the chalazal extremity, while at the micropyle end appear also the now newly-formed nuclei of the germinal vesicles (fig. 21), as three brighter, globular cavities, surrounded by dense granular mucilage (the vesicles imbedded in the protoplasm with more transparent fluid contents).

After the primordial utricle of the embryo-sac has also displaced that hollow conical layer of dissolving cells which covers its micropyle end, it becomes closely applied upon the now free enveloping membrane*. This adhesion is so intimate at the micropyle end, that in all subsequent stages the enveloping membrane seems at this point to have been secreted by the primordial utricle of the embryo-sac. Further down, from the region where the cavity enclosed by the inner integument and lined by the enveloping membrane (of the nucleus) becomes widened and expanded into a cylindrical form, the growth of the primordial utricle in breadth is frequently restricted; it then runs on as a slender cylinder in the axis of the wider. The tubular space between the enveloping membrane of the nucleus and the elongated primordial utricle of the embryo-sac is filled with finely granular mucilage coloured deep brown by iodine, probably the product of the solution of the liquefied peripherical cells of the nucleus (Pl. VII. fig. 23).

These processes are accompanied by a very considerable elongation of the embryo-sac and the enveloping membrane of the nucleus, which both integuments follow by a rapid multiplication of their cells in the direction of the length of the ovule.

* Formed by the persistent, connected outer walls of the superficial layer of cells of the nucleus (see above).—A. H.

The shape of the ovule becomes materially altered by this, passing from an ovate form into that of a cylinder with a slightly attenuated summit and a rather swollen base.

The lower persistent part of the nucleus is now pear-shaped. Its apex, as in *Crocus* and elsewhere, exhibits a funnel-shaped excavation, lined by the chalazal end of the embryo-sac, in which are confined the three "enigmatical antipodes of the germinal vesicles*" (fig. 23). The germinal vesicles themselves, now fully developed, pear-shaped and large, with the inside of their walls lined by a layer of protoplasm which encloses the now lenticular nucleus, bear a similar relation to the micropyle end of the embryo-sac (figs. 22–24). The primary nucleus of the latter has by this time disappeared: if the embryo-sac has become adherent at all points to the enveloping membrane of the nucleus, secondary nuclei of a lenticular form are now frequently found lying upon the inside of the wall of the former, and these are mostly the centres of slightly developed systems of radiating threads of granular mucilage (fig. 22). With the exclusion of an exceptional case occasionally occurring in *Z. minor*, to be mentioned hereafter, this is the only indication of a preparation for the production of endosperm met with through the whole existence of the ovule of *Zostera*. After fertilization these nuclei disappear again, without having arrived even at a transitory cell-formation.

The ovule is now ready for fertilization; during its development the mouth of the rudimentary ovary becomes prolonged into the canal of the style; the filiform stigmas spring out later through a more active multiplication of cells at two points of the circumference of the orifice. The styles, which turn upwards at obtuse angles, are protruded at the period of flowering from the slits of the leaf-sheath enclosing the inflorescence. The anthers burst at the same epoch; each half-anther opens by a longitudinal slit running up over the septum dividing the two loculi. The filiform pollen-cells arrive immediately upon the arms of the stigma projecting into the burst half-anthers. They are often found, singly or several together, spirally wound round these arms.

* A. Braun, *Die Erscheinung der Verjüngung*, &c. Leipsic, 1849 (1851), p. 297.

The end of the pollen-cell penetrates into the canal of the style opening at the summit of the two arms of the stigma. I was unable to lay free, uninjured from the stigma to the micropyle, the pollen-tube into which the otherwise already tubular pollen-cell is doubtless converted by continued growth of one of its extremities in the longitudinal direction. Within seven hours after the dehiscence of the anther, the pollen-tube is found in the cavity of the ovary*; adhering closely to the outer side of the pendent ovule, it grows down to its micropyle, into which it penetrates, suddenly making a sharp curve. The internal cavity of the ovary, now greatly enlarged by the expansion of its walls, is filled with transparent but tolerably firm jelly, in which may sometimes be distinguished swollen-up cells, not unlike those of the epithelium of the inside of the human mouth. They are perhaps detached cells of the conducting tissue. A little air-bubble is commonly found in the lower extremity of the cavity of the ovary, at the end opposite to the stigma.

The pollen-tube is of the same diameter as the pollen-cell (figs. 24–26). The portion outside the micropyle dies away rapidly; within this it remains perceptible for a considerable time. It does not usually penetrate farther than the summit of the embryo-sac, very rarely insinuating itself for a short distance down between this and the inner wall of the second integument.

After the arrival of the end of the pollen-tube at the outer wall of the embryo-sac, formed by the enveloping membrane of the nucleus, one of the germinal vesicles increases in size and its nucleus vanishes (fig. 24). The other germinal vesicles shrivel up (fig. 25) and die away; often even before the pollen-tube has emerged from the micropyle-canal. A newly-formed, globular or ellipsoidal nucleus soon makes its appearance in the lower end of the fertilized germinal vesicle, inside the mass of protoplasm accumulating there; immediately after this comes, above the nucleus, a septum, convex on the upper side, dividing

* Anthers of a plant of *Zostera marina* taken from the sea-water on the 4th of June 1851, opened before my eyes on the 7th of June at half-past 6 in the morning, after a land journey of more than forty hours. By one o'clock on the same day the pollen-tubes had penetrated into the micropyles of ovules of the same inflorescence. The plants had been kept ever since their removal from their habitat moderately damp (not wet), and excluded from the air.

the germinal vesicle into a small lenticular, lower cell, and a larger, expanded, upper cell (fig. 25). The latter contains no nucleus; a thin layer of granular mucilage coats the inside of its wall, and its cavity is filled with watery fluid. This upper cell is not further developed during the subsequent completion of the seed.

The little lower cell, on the contrary, at once enters upon a very rapid multiplication. It swells up into a flattened globular form, and divides by a longitudinal wall; both the newly-formed hemispherical cells then immediately divide into two "daughter-cells," having the form of quarters of a sphere, by septa standing at right angles to those just before produced. These four cells, constituting the rudiment of the embryo, are each divided by a horizontal cross septum (fig. 26). By continued halving of its cells, principally in the longitudinal direction, the flattened globular mass of cells (fig. 26) soon becomes spherical (figs. 27, 28); and finally, while constantly increasing in size, ovate and compressed laterally (fig. 29). The large spherical cell which supports it is only loosely attached to the inside of the wall of the micropyle end of the embryo-sac. I more than once saw the swollen cell, and the cellular mass sprung from it, slip from the micropyle end of the embryo-sac halfway towards the other extremity, without perceptible external cause*.

By the time the rudiment of the embryo has acquired the globular form, a single apical cell becomes distinctly visible (fig. 28), in the organ which in previous stages of development undoubtedly possessed four. This transformation may be aptly explained by the supposition that one of the four cells originally forming the apex divides into one inner and two outer cells; either by a longitudinal septum forming an angle of 45° with each of the two side walls of the cell, after which a radial longitudinal wall appears in the outer of the newly-formed cells; or by a longitudinal wall parallel to one of the lateral surfaces, the formation of which is immediately followed by that of another at right angles to it. If we further suppose that, in either case, the other three of the previously apical cells become divided by radial longitudinal septa, during the formation of one

* See the note to fig. 26 in the explanation of the figures.

inner and two outer in the fourth cell, the final result, under either hypothesis, would be the formation of a central (apical) cell surrounded by a chaplet of eight cells.

During the transformation of the smaller segment of the impregnated germinal vesicle into a globular cellular body, the enveloping membrane of the nucleus, which has become a tough coat of the embryo-sac, adheres most intimately to the inside of the inner integument. The edges of contact of the cells of the latter soon make marks upon the hitherto homogeneous, smooth membrane in the form of cellulose ridges running upon it; at first extremely delicate, scarcely perceptible, but gradually more distinct, and at last so sharp, that the wall of the embryo-sac most deceptively resembles, when seen only on the surface, a layer of tubular cells filled with transparent contents. The peculiar conditions of this enveloping membrane, its lengthened vital activity, its energetic growth, and its nutrition by the tissues and cells of different kinds which it encloses, deserve particular attention.

From one of the broad surfaces of the laterally-compressed, ovate rudiment of the embryo springs an obtusely conical projection of cellular tissue, the rudiment of the future principal axis of *Zostera*, which is thus a secondary axis, a lateral sprout of the leafless axis of the first rank, of the embryo. Very soon after the appearance of the new structure, the first leaf is developed, a little below its apex (figs. 30, 31, 33–35). This presents itself as a little ridge nearly surrounding the end of the stem, and very rapidly grows higher at the border turned to the chalaza, than at other parts. The leaf grows longitudinally through constant repetition of the division of a transverse row of apical cells, by walls inclined alternately towards the upper and lower surfaces of the leaf, and by division of the cells of the second degree by cross walls. The direction of its growth is parallel to the primary axis of the embryo, diverging at right angles from its parent axis.

During the development of this leaf, a very considerable alteration occurs in the shape of that axis of the first rank: by active multiplication of its cells, predominantly in the directions of breadth and length, the ellipsoidal cellular body becomes a flat mass truncated below and gradually attenuated toward the upper

and lateral borders (Pl. VIII. figs. 32, 35–37). The lateral borders at the same time curve over the anterior surface, so that they finally enclose, like a hood, the secondary leaf-bearing axis attached upon that surface. The multiplication of the cells, very active at all the edges of the cellular plate, lasts longest at the upper margin, directed towards the micropyle. The large cell, to which the embryo was previously suspended, becomes pushed very much to one side by this (fig. 32). Soon compressed by the further increase of size of the primary axis, it is in a short time lost sight of altogether.

The leaf-bearing axis, the lower, naked portion of which has meantime been extending upward with a considerable curvature, unfolds, soon after the protrusion of the first leaf, the second, opposite to that; the third becomes opposed to this higher up on the stem, and finally the fourth to the third (fig. 39). The greatly prolonged extremity of the stem grows by continued repetition of division of the single apical cell, by means of septa inclined alternately to the two surfaces of the leaf, division of the cells of the second degree by radial longitudinal walls, and so on; corresponding to the rule of cell-multiplication in the rudiment of the fruit of Mosses, of the *Marchantieæ*, the stem of Mosses, the stem of the Polypodiaceæ, the axes of the Equisetaceæ and *Pilularieæ*, and the young embryos of the Coniferæ. But, as in the Coniferæ, the rule of cell-formation changes subsequently, after the germination of the seed. The one apical cell of the now obtuse, flattened terminal bud (fig. 40) divides by walls inclined successively to the four points of the compass, in agreement with the rule of cell-multiplication in the further developed rudiment of the fruit of *Anthoceros**.

Buds appear in the axils of the older leaves even before the maturity of the embryo. Subsequently also, in the fully-developed, annual sterile plant, the formation of an axillary bud follows that of the leaf almost immediately (Pl. VIII. fig. 40).

In the foregoing I have called the cellular body, formed by the increase of the lower segment of the impregnated germinal vesicle, which is finally transformed into a hood-shaped layer of cellular tissue, *the axis of the first rank*, of the embryo. Older botanists regarded it as the cotyledonary leaf,—a view which

* See page 6 of my *Vergleichende Untersuchungen*, &c. Leipsic, 1851.

Grönland also supports, although A. de Jussieu*, so long ago as 1838, demonstrated that this is untenable, by comparison with other Monocotyledonous embryos, and explained the organ as a transformation of the plumule (*tigelle*) of the embryo, without however recognizing the leaf-bearing stem as a secondary axis. An unprejudiced examination of the course of development completely refutes the older view. But even if it were assumed, for the sake of the pretended analogies, that the direction of the main axis of the embryo underwent a division not to be detected by actual observation; that the cell of the lateral surface of the flattened-ovate cellular body, which gives origin by its cell-multiplication to the leaf-bearing axis, was the twelfth cell of the first degree of the embryo, and that the obtuse end of that cellular mass underneath this cell was the rudiment of the cotyledon,—the cotyledon and the next succeeding leaf would be made to stand in one perpendicular line, *i. e.* the leaf directly over the cotyledon; a supposition incompatible with the phænomena exhibited in the after-life of *Zostera*.

There is no example among all the Dicotyledons of the principal leaf-bearing stem of a plant being an axis of the second rank, the lateral sprout of a leafless primary axis. The development of the embryo of *Tropæolum*, which at first sight appears similar to that of *Zostera*, differs from it most essentially in the circumstance that the portion of the pro-embryo, from the end-cell of which the embryo originates, is in *Tropæolum* the primary axis, only crowded to one side by the more vigorous development of the peculiar lateral sprout of the pro-embryo†.

Among the Monocotyledons there is one plant, *Ruppia rostellata*, resembling *Zostera* in many characters of its subsequent life, which may be compared with the latter, in reference to the characters of the embryo, without straining any point. The ovule of *Ruppia* agrees in structure with that of *Potamogeton*. Like that, it completely resembles the ovule of *Zostera* in its early development, in attachment, direction and shape (fig. 41 *a*, *b*). But that large cell in the interior which becomes the embryo-sac, only displaces a moderate portion of the nucleus before impregnation; the outer layers of cells of the latter persist (fig. 42). As in *Potamogeton*, the previously concentrically-shaped ovule begins

* *Ann. des Sc. Nat.* 2 sér., *Botanique*, tom. xi.

† See my essay *Die Entstehung des Embryo*.

to assume a symmetrical form shortly before impregnation. The micropyle becomes pushed downwards by active multiplication of the cells on its outer side, turned away from the contiguous angles of the four ovaries (fig. 42). A multiplication of the cells of the opposite side of the nucleus commencing at the epoch of impregnation, subsequently pushes the micropyle upwards again with a great curvature of the entire ovule (fig. 43). The integuments follow the increasing size and changing shape of the ovule by multiplication of their cells in the directions of length and breadth. After impregnation the process of multiplication and expansion of the cells becomes very unequal, especially on the inner coat of the ovule: much more active in the lower than in the upper half, it pushes the endostome still farther upward (fig. 44), and removes it from the endostome, which remains nearer its original place, and consequently becomes diverted to the side.

The impregnated germinal vesicle of *Ruppia* divides, as in *Zostera* and *Potamogeton*, into a larger, upper, persistent cell and a smaller, inferior cell which undergoes rapid multiplication. During the gradual removal of the papilla (apex) of the nucleus and of the endostome from the place of the germinal vesicle, the pollen-tube, which remains outside the membrane of the embryo-sac, extends itself, inside the place where it penetrates, through the apex of the nucleus, by means of considerable longitudinal growth of its tough membrane (fig. 43 *b*).

The lower segment of the impregnated germinal vesicle very soon becomes changed, by a series of longitudinal and transverse divisions (figs. 43 *b*, 44 *b*), into a globular and subsequently an ovate cellular body (fig. 45 *b*), from the side of which, below the apex, shoots forth the first leaf-bearing axis. It unfolds its first leaf close above its point of origin. After the imbedding of the base of the leaf-bearing axis in the thick, fleshy, primary axis, the first adventitious root grows out, in germination, opposite the lamina of that first leaf (the cotyledon), forming a right angle with the line of direction of the leaf. The margins of that lateral face of the primary leafless axis which bears the leafy secondary axis, rise up into a kind of collar, enclosing the base of the latter as a short, widely opened sheath (fig. 46).

Irmisch*, in a clear explanation of the subsequent course of the

* "On the Inflorescences of the German *Potameæ*," Flora 1851, p. 81 *et seq.*

germination of *Ruppia*, has already drawn particular notice to the fact, that the germination not only of *Potamogeton*, but of all the grasses in which the first leaf stands before the *scutellum*, agrees in the main points with that of *Zostera*. The history of development of these embryos, far from weakening the foundation for such an interpretation of the individual parts, rather speaks more distinctly in favour of the so-called *scutellum* of the embryos of *Zea* and *Sorghum* being analogous to the first, leafless axis of *Zostera**.

The course of development of the embryo of other Monocotyledons, so far as known, gives still further probability to the idea that the "cotyledon" is an axis with limited growth, from the side of which breaks forth a sprout, the future leaf-bearing main axis of the plant. I refer to the history of development of the embryo of *Canna*† given by Jussieu, with which completely agree, besides those of the plants mentioned by Jussieu himself, those of *Hyacinthus comosus*, *Funkia cærulea*, *Fritillaria imperialis* and other Liliaceæ, that of *Iris* and others. In all cases the first cell of the embryo (the lowest cell of the pro-embryo forming the suspensor) becomes converted by a series of divisions into a globular, ovate or spindle-shaped cellular body, the increase of thickness of which is arrested at a point below the summit. Thus is formed a lateral, more or less deep slit, from the bottom of which is developed the plumule, in one case (*Fritillaria*) not till after germination. No fact is less available as testimony against the axial nature of the so-called cotyledon of the Monocotyledons, than that of its base enclosing the plumule as a sheath. If the secondary axis originates at a point on the primary in which the growth in thickness of this latter is arrested some time before the appearance of the lateral sprout, the encompassing of the new axis by the thickened borders of the

* See figures 12–14, 32–34 of Pl. xi. of my Essay *Die Enstehung des Embryo der Phanerogamen*. At the time when I published those researches, not yet enlightened by the study of the formation of the embryo of the Naiadeæ, I thought myself obliged to adhere to the view advocated by Bernhardi, Schleiden and Jussieu, although it did no little violence to the phænomena observed. The papilla of cellular tissue becoming the plumule, appears from the first distinctly lateral and below the apex of the nascent "cotyledon," in these grasses, as also in the *Avenaceæ* and *Triticeæ*.

† *Loc. cit.* p. 348.

lateral surface of the older sprout naturally follows; as occurs most clearly in the earliest rudiments of fronds, situated in depressions of the creeping main axis, of *Polypodium aureum* and other Ferns. But even secondary axes which become nakedly visible on the originally convex outer surface of the young main axis, may likewise become sheathed subsequently by the primary sprout, through peculiar growth of the latter; *Isolepis* affords a striking proof of this.

It need scarcely be explained that the discussion here promulgated is not and could not be anything more than an invitation to repeated investigations of the different stages of development of the Monocotyledonous embryo. A complete decision in favour of one or other of the two views can only be obtained by tracing back—a difficult task indeed—the development of the seedling plant to the mode of increase of each individual cell.

No question in the whole field of the Morphology of Plants has been treated by so many persons and in such varied ways, as the import of the parts of the embryo of the Monocotyledons; to none better applies an often misplaced quotation from Goëthe; we may assert that "all possible combinations are exhausted" here. Thus the idea brought forward in the foregoing pages is only the repetition of an earlier one essentially similar. If it be thought better grounded than that more current among modern botanists, we find, in recompense for the wide separation it makes between the Dicotyledons and Monocotyledons, the most striking agreement of the development of the embryo of the latter, with the course of the formation of the germling of the Vascular Cryptogamia. As I have abundantly demonstrated*, the main stem of the plant of all Vascular Cryptogams is a secondary axis, arising laterally on the primary leafless axis. A second and not unimportant point of comparison then at once suggests itself. The Vascular Cryptogams may be divided into two primary groups according as the germinating plant produces the second frond below the first (below that surface turned away from the mouth of the archegonium), or above it. In the former case the first adventitious root appears simultaneously with the first frond, beside its base; in the latter case,

* See *Botanische Zeitung*, 1849, p. 797; "*Vergleichende Untersuchungen*, &c." Leipsic, 1851, pp. 85, 106, and elsewhere.

opposite to it. The Ferns and Rhizocarpeæ belong to the first of these sections, *Selaginella* and *Isoëtes* to the second. The peculiar arrangement of the roots of *Isoëtes* does not follow so much from the condition just indicated, as from the phænomena of the growth of the mantle of cambium, annually renewing the cortical tissue, surrounding the wood-structure; combined with the suppression of the internodes. In *Zostera*, *Ruppia*, and in the Grasses, the mode of appearance of the first adventitious root is the same as in *Isoëtes*. It springs out opposite the first leaf, not behind it. The great majority of the Monocotyledons seem to behave in the same way. In *Lemna*, on the contrary, the position of the first adventitious root corresponds to that of the Ferns. To carry through the comparison of the two classes in this respect will require still more comprehensive researches.

EXPLANATION OF PLATES VI, VII and VIII.

Fig. 1. Longitudinal section of the terminal bud of a fertile plant of *Zostera minor*, magnified 30 diam. :—*a* the third, *b* the second, *c* the first (youngest) spadix; a^1, b^1, c^1, the sheathing basal leaves (*niederblätter*) of the sprouts terminating as spadices; a^2, b^2, c^2, the stem-leaves (*laub-blätter*) of the same; *d*, the new sprout arising in the axil of the sheathing leaf of the youngest sprout.

Fig. 2. A similar preparation of *Zostera minor*. The section, not carried quite accurately through the slit of the sheathing leaf of the sprout of the penultimate rank, has hit the overspreading part of this sheath.

Fig. 3. Apex of a spadix of *Z. marina* commencing a longitudinal development, seen from above. Magnified 40 diam. :—*a*, anthers; *b*, ovaries.

Fig. 4. Young anther (*a*) and rudiment of an ovary (*b*) of *Zostera minor*, seen from above. Magnified 120 diam.

Fig. 5. Transverse section of a very young half-anther of *Z. minor*. Only the contents of the primary parent-cell of the pollen represented. Magn. 350 diam.

Fig. 6. Similar preparation from a somewhat more developed anther. Magn. 350 diam.

Fig. 7. Some of the primary parent-cells of the pollen, from the longitudinal section of a very young half-anther of *Z. marina*. Magn. 400 diam.

Fig. 8. Lower portion of a longitudinal section of a half-anther of *Z. marina*, parallel to the surface of the spadix; *a*, cells of the septum between the two loculi. Some of the elongated parent-cells of the pollen cut across. Magn. 400 diam.

Fig. 9. Portion of the longitudinal section of a half-anther of *Z. marina* immediately after the formation of the pollen-cells. Magn. 400 diam.

Fig. 10, 12. Transverse sections of loculi of somewhat more developed anthers of *Z. minor*. Magn. 200 diam.

Fig. 11. A collection of young pollen-cells of *Z. marina*. Magn. 400 diam.

Fig. 13. A few somewhat further developed pollen-cells of the same species, isolated in concentrated solution of carbonate of ammonia. Magn. 400 diam.

Fig. 14. Longitudinal section of the lower part of an anther-loculus of *Z. minor*. Magn. 300 diam.

Fig. 15. Piece of a mature pollen-cell of *Z. marina*. The ascending current of protoplasm is shown darker, the descending lighter. Magn. 400 diam.

Fig. 15 *b*. Pieces of mature pollen-cells exhibiting protrusions of all kinds (see page 245). Magn. 200 diam.

Fig. 16. Very young ovaries of *Z. marina*, seen from above; *a*, rudiment of the ovule. Magn. 300 diam.

Fig. 17, 18. Subsequent stages of development of the ovary, in longitudinal sections. Magn. 100 diam.

Fig. 19. Ovules and the surrounding parts of the walls of the ovary, in longitudinal section. Magn. 320 diam. The pendent ovule is here represented reversed and upright, as in all the succeeding figures.

Fig. 20, 21. Longitudinal sections of the nuclei of more developed ovules. Magn. 300 diam.

Fig. 22. Longitudinal section of an ovule ready for impregnation. The formation of the cells compressed into the chalazal end of the embryo-sac has not taken place here. Magn. 320 diam.

Fig. 23. Longitudinal section of an ovule of the same species ripe for impregnation. Magn. 180 diam.

Fig. 24. Micropyle and upper end of the embryo-sac of an ovule in longitudinal section, at the moment when the pollen-tube has penetrated to the membrane of the sac. Magn. 300 diam.

Fig. 25. A similar preparation, a little later, with the impregnated germinal vesicle divided into an upper, large suspensor cell, and a lower, small embryonal cell. Mag. 300 diam.

Fig. 26. A similar preparation with the embryonal globule, composed of 16 cells, represented in longitudinal section. During the observation the suspensor and the embryonal globule slipped from the micropyle end of the embryo-sac as far as *, without perceptible external cause. Magn. 300 diam.

Fig. 27. Lateral view of a further developed embryonal globule with the suspensor. Magn. 400 diam.

Fig. 28. A similar embryonal globule, in longitudinal section, at right angles to the projection of the preceding figure. Magn. 400 diam.

Fig. 29. Front view of an embryo with suspensor of *Z. minor*, shortly before the origin of the leaf-bearing axis. Magn. 60 diam.

Fig. 30. Lateral view, 60 diam.; fig. 31. front view, of farther developed embryos of the same species. Magn. 40 diam.

Fig. 32. Lateral view of the embryo of a half-ripe seed of the same species. The outline of the secondary axis is indicated by delicate lines, showing through the lateral wing of the primary axis. Magn. 40 diam.

Fig. 33–35. Embryos of *Z. marina*.—Fig. 33, side view of a young embryo; fig. 34, front view of one somewhat older; fig. 35, seen obliquely from behind. Magn. 40 diam.

Fig. 36. Longitudinal section of a half-developed embryo. Magn. 30 diam.

Fig. 37. Longitudinal section of an almost ripe embryo. Magn. 30 diam.

Fig. 38. Ripe embryo, in front, back and lateral views. Magn. 4 diam.

Fig. 39. Longitudinal section of the bud of an almost ripe embryo. Magn. 60 diam.

Fig. 39 *b*. The end of the stem of the same. Magn. 300 diam.

Fig. 40. Longitudinal section of the terminal bud of a sterile plant of *Z. marina*.

Fig. 41–46. *Ruppia rostellata*.

Fig. 41. Longitudinal section of a young ovary. Magn. 40 diam.

Fig. 41 *b*. The ovule of the same. Magn. 200 diam.

Fig. 42. Longitudinal section of an ovule ready for fertilization. Magn. 60 diam.

Fig. 42 *b*. Embryo-sac of the same. Magn. 300 diam.

Fig. 43. Longitudinal section of an ovule immediately after impregnation. Magn. 40 diam.

Fig. 43 *b*. Endostome, papilla of the nucleus and micropyle-end of the embryo-sac of the same. Magn. 300 diam.

Fig. 44. Longitudinal section of an ovary, some eight days after fertilization. Magn. 30 diam.

Fig. 44 *b*. The rudimentary embryo of the same. Magn. 200 diam.

Fig. 45. Longitudinal section of a farther developed ovary. Magn. 30 times.

Fig. 45 *b*. The embryo from it. Magn. 200 diam.

Fig. 46. Longitudinal section of an almost ripe embryo. Magn. 40 diam.

[A. H.]

Article IX.

On the Winding of Leaves. By M. Wichura.

[From the '*Flora*,' January and February 1852.]

THE leaves of plants possess in the flexibility of their tissue full capability of twisting, and it has long been known that this property must often serve to assist the efforts of plants to approach towards the light. Twisting movements of this kind are readily recognizable from the circumstance that all the characters of the movement may be brought into agreement with their purpose, to direct the upper face of the leaf towards the light. The twisting begins directly anything turns the upper face of the leaf away from the light, and continues until that face is again directed to the full rays of the incident light. It turns indifferently either to the right or left, according to which path will lead quickest to its object. Its extreme degree never exceeds a half-revolution, since this suffices to turn the leaf completely over, and therefore to return the upper side again towards the light, when it has been wholly turned away from it.

But there are plants the winding leaves of which present exactly the opposite character in all these things, and, in particular, exhibit the same regularity in their lateral direction as we detect in winding stems.

The winding movements of the second kind cannot be regarded as an effect of the irritability of vegetable tissue excited by light. They are immediate expressions of the vital force active in the interior of the plant, and nearly allied to the winding of the stem and tendrils. While, however, the latter have long occupied the attention of botanists, the windings of leaves have remained almost unknown, and all that we possess are a few scattered and mostly very meagre notices thereon. I myself gained my first knowledge of them through perceiving the heliacal winding of the leaves and strict regularity displayed in their direction, in some Oat and Barley plants germinating indoors. Further researches, to which I was thereby attracted,

made partly in the field, partly in the Botanical Gardens of Breslau and Berlin, and lastly, partly in the General Herbarium at Berlin, have revealed to me so great a number of similar phænomena, that I venture to found upon them an attempt at a general description of the phænomenon.

I. *Form and outward condition of Winding Leaves.*

§ 1.

Although examples of winding leaves may be pointed out in all metamorphoses of the leaf, in the most diverse families of the vegetable kingdom, and in all the local floras of the globe, much agreement in structure is exhibited by them in spite of this wide diffusion. They are all of longish, mostly linear-lanceolate shape, have smooth entire margins, and in regard to the distribution of their vascular bundles, either belong to the parallel-nerved system, as developed most clearly in the stem-leaves of Monocotyledons, or they are totally devoid of vessels, as in the leaves of the Mosses and Liver-worts. The angular-nerved leaves of the Dicotyledons, as for instance of our fruit-trees, of the Poplar, Lime, &c., appear never to admit this winding movement. In the Dicotyledons only those leaves wind which imitate, either perfectly or at least approximatively, the parallel-nerved system of the Monocotyledons.

§ 2.

If we attempt to bring the properties of winding leaves, mentioned in the preceding section, under a common point of view, we must say that the longitudinal growth is developed at the cost of the transverse growth in winding leaves. For, if the angular-nerved distribution of the veins in which strong branches turn off toward both sides from the midst of the leaf, and, suddenly leaving the longitudinal direction, pass into the transverse, is to be considered, no less than the lateral subdivision of the leaf into teeth, pinnæ, &c., as the expression of an active growth in the direction of the breadth,—it follows that the essential feature of leaves which neither have an angular venation, nor are toothed or pinnate, but are parallel-veined, smooth-edged and very narrow in proportion to their length, must be a

deficiency of transverse and an excess of longitudinal growth. Winding leaves agree perfectly in this respect with winding stems and tendrils, the thread- or string-like shape of which at once reveals the predominance of longitudinal growth.

§ 3.

Another peculiarity of winding leaves might be sought in the distribution of their stomates. In the ordinary, not winding leaf, they are chiefly placed on the lower face, next the ground, in order, as is supposed, to come, in this way, into immediate and close contact with the gases and vapours ascending from beneath. A differently contrived distribution of the stomates should consequently be provided for winding leaves, which by their curvature often change the relative position of their two faces toward the vicinity. This conjecture finds a very striking confirmation in the stem-leaves of the *Alstrœmeriæ*, which turn quite over by a half-revolution, for, according to the beautiful observations of Lindley, these bear the stomates, contrary to the ordinary rule, on the upper face, turned towards the ground only by the twisting. The winding leaves of the Grasses also, as I have had an opportunity of observing, present anomalies, in so far that they are furnished with stomates almost equally on both sides of the leaf. Unfortunately I was unable to extend these somewhat 'time-devouring' researches to other families. I can therefore only offer a conjecture that winding leaves are distinguished from those not winding by a more or less aberrant distribution of the stomates.

§ 4.

In other respects, winding leaves present little that is striking in their external appearance. Not twining round a support like winding stems, they complete their curvatures in the free air, and from their slender, linear form, one is at first sight inclined to ascribe their curvature to accidental effects of the wind and of desiccation. The detection of the regularity prevailing in their direction unfolds the error of the supposition, and opens to our view a rich and everywhere ready field of observation, where we previously passed by in indifference.

II. *Laws of Distribution.*

§ 5.

The relation of the winding to the outer form of the leaf, mentioned in section 1, gives the key to the laws of distribution of the phænomenon. All alterations in the form of the leaf connected with the proportion of the longitudinal to the transverse growth, are consequently of importance in regard to the occurrence of the winding movement.

§ 6.

Even the single leaf displays changes of shape of this kind, in its triple division into sheath, stalk, and blade. Winding occurring in one of these parts is not therefore necessarily imparted to the others, but is mostly limited within this. There are many leaves with wound petioles and straight laminæ, while, on the contrary, in the stamens of *Erythræa* and other plants, the lamina metamorphosed into an anther winds, while the petiole, *i. e.* the filament, remains straight. Even within the lamina itself, modifications of the curving movement occur, with the expansions and contractions advancing from below upwards. In such cases only the narrow parts wind, the broader not. The broad ovate leaves of *Paris quadrifolia*, L., may be mentioned as an example, being straight as far as the attenuated points which are wound slightly to the left. Leaves which wind uniformly throughout their whole extent, exhibit the corresponding perfect equality of transverse growth, from bottom to top, as for instance the leaves of *Typha latifolia*, L., *T. angustifolia*, L., and of many other Monocotyledons.

§ 7.

The distribution of the winding movement in the different leaves of the same axis depends on the same principles. Here it is the metamorphoses of the leaf, known under the names of cotyledons, stem-leaves, sepals, &c., which limit the winding movement in virtue of their frequently totally different shapes. It very frequently happens that the winding of the leaves is

confined to a single metamorphosis, or that when the leaves of several metamorphoses wind, the intervening metamorphoses which do not wind, are separated from each other. In many species of *Dianthus*, for instance, the stem-leaves, the petals and the styles wind. Between these lie the metamorphoses of sepals and stamens, which do not betray a trace of the winding movement.

Winding and straight leaves are found united, even within the single metamorphosis, when the form of the leaves belonging to this metamorphosis is essentially altered from below upward, or according to the position which they occupy on the axis. Thus, for example, in *Papyrus antiquorum*, Willd., the lower, rather broad stem-leaves do not wind, but the upper narrow linear leaves preceding the inflorescence as bracts do. In many irregular flowers likewise, only single leaves, mostly outwardly conspicuous for prominent longitudinal growth, exhibit winding, for example the labellum of *Himantoglossum hircinum*, Rich. Here belong, moreover, the so-called oblique flowers, *e. g.* of *Hyssopus lophanthus*, L., *Pedicularis palustris*, L., &c., the oblique shapes of which arise from particular organs only of the flowers curving, and thus destroying the symmetry of the whole. Finally, the twisted awns of the Grasses must also be mentioned here, since in all cases they occur only in one of the paleæ forming the floral envelopes.

§ 8.

The distinction in the shape of leaves belonging to relatively like metamorphoses of different individuals, is fixed by the systematic distinctions in the vegetable kingdom. The more widely two species stand apart, systematically, the larger is the sphere of possible differences in the development of the leaf, the smaller therefore becomes the probability that they will behave similarly in reference to the movement of winding. The divisions into Cellular and Vascular Plants, Monocotyledons and Dicotyledons, founded on the most general distinctions in the vegetable kingdom, are consequently of no particular value for our purpose, since each of these divisions includes formations of leaves of the most varied kinds. It can only be said that the stem-leaves of

the Monocotyledons occur wound much more frequently than the stem-leaves of the Dicotyledons, on account of their structure being peculiarly suited for the movement of winding.

§ 9.

It is only when we come to the families of plants that it becomes possible to sketch out general characteristics of the natural divisions, in reference to the movement of winding. There are families in which I have not hitherto detected a single example of a winding movement, as for instance the Umbelliferæ and Cruciferæ; families in which the winding is confined to particular genera or species, as in the Compositæ and Papilionaceæ; and, finally, families in which the curvature of the leaves is typical, as in the Ebenaceæ, Apocynaceæ and Asclepiadaceæ.

The same holds good of the genera, with the distinction that a complete agreement of the species included in them is much more frequent than in the families.

In general, the behaviour of the individuals belonging to the same species is identical. Deviations are rare, and seem only to arise when the shape of the leaves has undergone a material change through the influence of the station. Thus I found in a hot-house a specimen of *Hyacinthus orientalis*, raised in rich earth, in which the stem-leaves had attained the unusual length of $2\frac{1}{2}$ feet, and were twisted, while under ordinary circumstances the leaves of this plant do not wind.

§ 10.

Finally, peculiarities of the soil and climate also have to be mentioned among the causes of the diffusion of the phænomenon, since these sometimes give a particular character to the habit of the plant, and especially to the prevailing form of the stem-leaves. Thus, tropical America is remarkable for an abundance of plants with broad leaves with reticular venation, in which the here incompatible movement of winding withdraws from notice, and, considered in relation to other regional floras, becomes rare. On the other hand, the floras of New Holland and the Cape of Good Hope contain principally plants with narrow, parallel-nerved stem-leaves, and it is to be regarded as a consequence of this, that Dicotyledonous plants with winding stem-leaves occur

comparatively much more frequently in these two regions than in the other parts of the globe.

III. *Single and associated Winding Leaves.*

§ 11.

The phænomenon of winding is not confined to the single leaves of plants, but appears also in structures arising from the confluence of several leaves. Longish shape and parallel course of the vascular bundles are also conditions here. For example, the tubes of the corollas of several Stylideæ, which may be called rather long in proportion to their diameter, those of *Trifolium resupinatum*, L., and certain species of *Peristrophe* and *Hypoëstes* of the family of Acanthaceæ. So, moreover, the elongated buds of the Convolvulaceæ and of *Thevetia neriifolia*, Juss. (Apocynaceæ), originally composed of five separate and very narrow segments, are folded toward one side like a closed umbrella and curved spirally toward the other, &c. If the view, now continually gaining ground, that the stem is not an independent organ, but originates from the confluence of the sheathing portions of the leaves fitted into each other, could be regarded as completely demonstrated, the winding stem also would have to be included here.

§ 12.

After these examples of winding of several confluent leaves, we may come to those which certainly wind separately, but are situated so close together that they come in contact in the movement of winding, and in this way enter into certain combinations, which, from the regularity of the movement on which they depend, assume a regular shape.

§ 13.

Here belong: the entwined cotyledons of the Gyrocarpeæ; the awns of the panicles of *Streblochæte nutans*, Hochst., and *Andropogon Allionii*, D.C., which are twisted together into a cord-like body; the floral envelopes of many species of *Iris* and all the species of *Aristea* (Iridaceæ) known to me, which wind round

spirally as the flower withers; and lastly, what is called the "contorted æstivation." The latter deserves a separate discussion, because its connection with the winding movement is not at first sight clear.

§ 14.

The "æstivatio contorta" is a structure which makes its appearance at a comparatively late stage of the growth of the bud. When examined in their earliest conditions the rolled buds exhibit leaflets standing singly, so narrow that their margins do not touch. They become broader at a later stage, and the position of the leaves, peculiar to the twisted æstivation, arises from the mutual over- and inter-growth of their margins.

Fig. 1, Pl. IX. represents two horizontal sections of oppositely rolled buds. By an examination of these it is readily ascertained that the surfaces of the leaves are obliquely inclined to the centre of the flower, and in the same direction in all the leaves of the same flower. Either the leaves have been attached obliquely on the receptacle from the first; and then the twisted æstivation is not the effect of a subsequent twisting of the separate leaflets, and does not belong here; or the leaflets are not originally attached obliquely; and then they can only be brought into the oblique position subsequently evident, by a slight twisting. Which of these two alternatives is the correct one, I could not ascertain by direct observations, since the oblique position of the leaflets only becomes perceptible by its effect, the growth of the borders over and between each other. It is so slight, and the curvature, if such occurs, is so lost in the earliest stages of the bud, that it sinks to a microscopical magnitude, from the transparency and delicacy of all the parts no longer recognizable by the sight. On the other hand, conclusions may be drawn from other perceptible facts, which give very reliable testimony that the twisted æstivation owes its origin to a winding of the individual leaflets.

§ 15.

In the first place, an approximative testimony is furnished by the occurrence of the twisted æstivation in gamopetalous corollas. The history of development of these, teaches us that they

are composed, in the earliest periods of their formation, of separate leaves which subsequently become blended together. It will be admitted that if the "æstivatio contorta" depended on an oblique attachment of the leaflets upon the receptacle, this must exist from the moment of the origin of the leaf, and consequently in those earliest periods of growth when the individual parts of the gamopetalous corolla were not yet confluent. If then, in the "æstivatio contorta," the oblique position of the leaflets subsequently caused their borders, with the increasing breadth, not to meet together, but to pass over and under one another, this obliquity must, at the time when the confluence of the separate foliaceous elements should commence, hinder their coming into contact and consequently the confluence itself. Hence oblique attachment of the foliaceous elements and gamopetalous growth seem to exclude each other, and if gamopetalous corollas nevertheless do occur with rolled segments, it follows that the rolled position in the bud cannot be explained by an originally oblique attachment of the leaves. Then there only remains the other alternative, that the foliaceous elements are originally evenly attached, and only after confluence has occurred, undergo a twisting of the free points, by which they are brought into the position suited to the formation of the contorted æstivation.

§ 16.

I regard this proof as not wholly conclusive, only because it is based upon suppositions which relate to the still somewhat problematical processes of the confluence of the floral organs in the earliest stages of development of the flower. But the twisting of the leaflets on which the contorted æstivation depends, was completely demonstrated by an observation which I had an opportunity of making on a plant of *Helicteres* cultivated in the Berlin Botanical Garden. The long and narrow petals of this plant possess two opposite teeth on the margins, near the lower part. In the bud, the teeth of the adjoining petals cover one another in the manner of the "æstivatio contorta," as do likewise the upper parts of the little petals, but in an opposite direction. While the right tooth of one leaf covers the left tooth of the next leaf, the left margin covers, above, the right margin

of the next leaf. It is clear that this contrast cannot be explained by an oblique attachment of the young petals, since this can only act in one direction: we are absolutely compelled to the assumption that a curvature must have taken place here, which, as we shall see, in many cases alters its direction within the same leaf.

§ 17.

The rolled buds also betray their close relationship with the movement of winding in other respects. A comparatively very large proportion of the plants in which the floral envelopes or segments of the flower twist after the flower has opened, have rolled buds; for example: *Puya cærulea*, Miers (Bromeliaceæ), *Christya speciosa*, Ward and Harv., *Strophanthus divergens*, Graham (Apocynaceæ), *Pergularia edulis*, E. M., *P. accidens*, Blume, *Diplolepis Menziesii*, R. & S., *Oxypetalum riparium*, H. B. K. (Asclepiadaceæ), *Cyclamen europæum*, L., *Lysimachia punctata*, Wall. We likewise frequently meet with rolled buds which are at the same time twisted in one or other direction, as in *Æchmea latifolia*, Kth. (Bromeliaceæ), *Strophanthus dichotomus*, D.C., *Echites longiflora*, Desf. (Apocynaceæ), *Pergularia edulis*, E. M., *Microloma sagittata*, R. Br. (Asclepiadaceæ), *Gillenia trifoliata*, Mœnch. (Rosaceæ), &c. From all these reasons, therefore, I have no hesitation in regarding the "æstivatio contorta" as an effect of the movement of winding.

IV. *Heliacal shape of Winding Leaves.*

§ 18.

The characteristic mark of all winding leaves is their heliacal shape, with manifold modifications, however, depending on the variability of the distance of the heliacal line from its axis, the angle of inclination, and the length of the helix.

§ 19.

The distance between the heliacal line of the leaf and the axis of the helix may be either great or small. If it is reduced to the smallest possible amount, it coincides with the median line of the leaf itself. The fruit of *Ailanthus glandulosus*, L., repre-

sented in figure 3, may serve as an example. If we draw a straight line from the extreme point of this to its stalk, it will cut through the substance of the leaf in its whole course. The parts of the fruit lying in this direction consequently form a straight line and consequently the fixed axis, around which the halves on the right and left appear wound in the shape of a screw.

But if, on the contrary, the axis of the helix which the leaf describes lies outside the latter, all parts of the leaf share in the heliacal winding, and the leaf then resembles a band wound in a heliacal direction round an invisible cylinder or cone, where one side of the band is always turned towards the said cylinder or cone. The axis of the heliacal winding in this case coincides with that of the imaginary cylinder or cone. Leaves of this kind occur much more frequently than the others. Some examples are represented in figures 8 & 9.

§ 20.

The angle of inclination of the heliacal winding, *i. e.* the angle formed when a line is drawn through the helix parallel to its axis, is in many leaves so small as to be imperceptible, for example in the "æstivatio contorta;" in others it rises, judging from simple inspection, which indeed leaves a wide field for error, to 30°, 40°, or even 45°. It therefore falls short of 90°, the highest degree mathematically possible, which would flatten the helix into a plane.

§ 21.

Lastly, the length of the helix is dependent on the length of the leaf, or when only a part of this winds, on the length of this portion.

§ 22.

The sum of all these elements of the helix gives the number of revolutions. The magnitude of the angle of inclination and the length of the helix stand in direct, and its distance from the axis in inverse, proportion thereto. The greater the angle of inclination and the longer the helix, the higher the number; the greater the distance of the helix from the axis, the smaller the number of revolutions. Under otherwise like circumstances a broad leaf can never complete so many revolutions as a narrow one, because the

1
b
b'
c'
a'
a''
b''
c''
d
c

2

3
a
b'
b
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b''
a''

b
4
a

5

6

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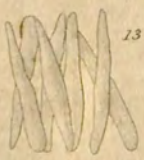
11

12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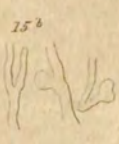
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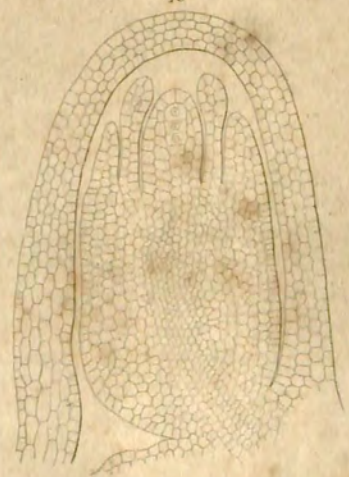
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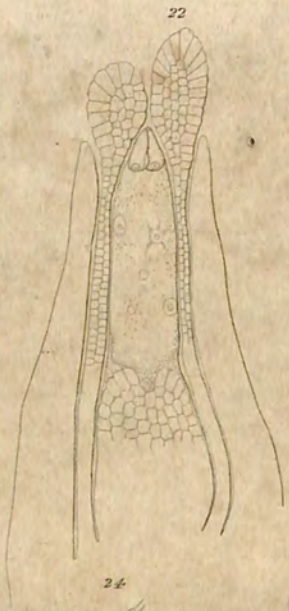
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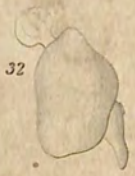
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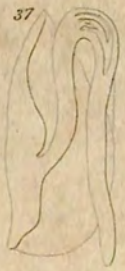
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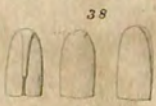
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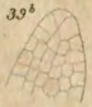
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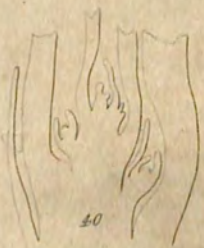
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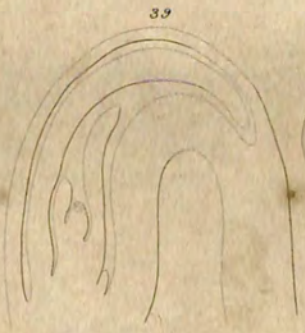
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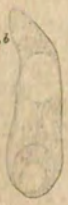
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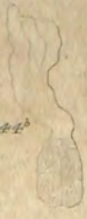
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helices which the margins of the leaf describe, at the same time as the other parts, must be further removed from the axis in the broad than in the narrow leaf.

§ 23.

Consequently the greatest number of revolutions, from twenty to twenty-five or even more, are found in the narrowest leaf-structures, *e.g.* in the awns of the Grasses, the leaves of many species of *Gethyllis*, &c., while elsewhere the most common number of revolutions is from $\frac{1}{4}$ to 2. Although accurate predetermination is mostly impossible here, since the length and breadth of the leaf, which influence the number of revolutions, usually vary in the same plant, still at least approximative determinations may be given for each species, and it is to be desired that descriptive botany should include this in the subjects of its observation. In flower-stalks which, as regards size and shape, appear always more constant than the stem-leaves, the number of revolutions of the heliacal windings admits of a tolerably exact definition.

V. *Rapidity of the Movement and Epoch of its Commencement.*

§ 24.

The winding movement takes place either rapidly or slowly. In the appendages of the carpels which separate at the epoch of maturity in the Geraniaceæ, it is so rapid as to be visible to the eye. In the other cases with which I am acquainted, we can only conclude that a movement has taken place by recognizing after long observation that a change of place has occurred. Days or even weeks may elapse before the leaf has completed even one revolution.

§ 25.

In regard to the epoch of commencement, the movement is connected with the stages of growth of the plant. It here follows definite laws, which however differ very much in different plants.

§ 26.

The "æstivatio contorta" affords the earliest traces of the commencement of a movement of curvature. The extremely

slight winding occurs here, it must be assumed, at an epoch when the leaves are still quite imperfect, in fact scarcely visible to the naked eye.

But in all other cases the winding does not commence until the leaf has attained a certain magnitude and maturity. The upper parts, as the older, wind first, the lower then gradually follow. The winding of the older part likewise precedes that of the younger in winding stems. But as in stems the lower parts are older than the upper, while in the leaf the upper parts are the older, the movement advances from below upwards in winding stems, and in the leaf on the contrary from above downwards.

§ 27.

In addition to these cases of a gradual origin and progress of the movement, there are some in which the movement begins suddenly and exhibits a more rapid course throughout its whole duration. We then constantly observe that the stage of growth which makes the commencement of the movement, is otherwise of importance in the development of the plant. Thus the rather rapid winding of the legumes of *Medicago* commences after fertilization has taken place, that of the anthers of many plants after dehiscence, of the petals of *Cyclamen europæum*, L., and a number of other plants, after the flower has opened, of the flowers of most species of the genus *Aristea* as soon as they begin to wither, of the awns of *Avena fatua* and probably all other Grasses with twisted awns, at the beginning of the maturation of the seed, and of the appendages of the carpels of the Geraniaceæ after their separation from the carpophore.

§ 28.

The movement of winding is in all these cases a rather transitory phænomenon compared with the duration of the existence of the plant, but it leaves permanent effects upon the shape of the leaf. When a twisted leaf is unrolled, it returns to its position as soon as released. It becomes "set" in the movement which has taken place in it, and an unrolling and rolling up of the heliacal winding may be produced in long dead awns of the Grasses or in the fruit-stalks of Mosses, by unequal hygroscopic expansion or contraction of their parts.

VI. *Mechanical Constituents of the Movement: Revolution round the Axis and Curvature.*

§ 29.

The movement of winding is in all cases founded on a revolution of the leaf around the straight line which may be imagined to pass from the point to the middle of its base. I call this the axis of the leaf, to distinguish it from the axis of the helix, which, as we have seen, may lie outside the substance of the leaf. This revolution round the axis, with the resistance, increasing from the freely moveable point down to the fixed base of the leaf, which is opposed to it within the parts of the leaf itself, causes a change in the relation of the direction of the parts of the leaf to one another. Under its influence, the substance of the leaf, originally expanded in a rectilinear plane, becomes converted into a body wound in the form of a helix, within which only the median line of the leaf, as the fixed axis around which the two laterally situated halves revolve, retains its original position. The forms of twisted leaves mentioned in § 19, in which the axis of the heliacal winding coincides with the axis of the leaf, are consequently fully explained by the mere assumption of a revolution of the leaf round the axis.

§ 30.

Very frequently a curvature of the leaf is added to the revolution round the axis. Then a mixed movement is produced, whence result the heliacally wound leaves with the axis of the helix lying outside the leaf. That it is so may be strictly proved mathematically by the aid of analysis. But a conviction of the importance of the explanation given may be also readily obtained in the empirical way, by holding a riband-shaped piece of wax by one end, and twisting it around its long axis while curving it at the same time toward one of its flat surfaces. In this way are produced heliacal bands which agree in all essential points with the forms of leaf represented in figures 8 and 9.

VII. *Direction of the Movement of Curvature.*

§ 31.

The leaf may be curved, toward either the upper or lower face. It follows from the nature of the mixed movement produced by a combination of curvature and revolution around the axis, that the concave side of the curve is directed towards the inside of the heliacal winding, the convex looking outward. Wound leaves which are at the same time curved, are consequently divisible into those with the upper and those with the lower face turned to the inside of the winding.

§ 32.

Examples of both kinds of winding leaves occur in nature. To the first category belong, for instance, the stem-leaves of most of our Gramineæ and Liliaceæ, to the latter the acicular leaves of *Pinus sylvestris*, L., and the anthers of *Erythræa Centaurium*, L. An individuality of a peculiar kind occurred on an *Allium* transplanted from the Halle Botanical Garden to that of Berlin, which was cultivated in the latter in the years 1848–49 under the name of *A. simplex*, and perhaps still exists there. The two alternating series of opposite leaves of this plant were curved to one side in the earliest condition, in such a manner that in one series the upper and in the other the lower sides of the leaves formed the curved surface. If revolution around the axis is subsequently added to this, we get in one series leaves with the lower faces, and in the other leaves with the upper faces turned toward the interior of the helix. The two kinds of wound leaves elsewhere only found, in the same leaf-metamorphosis, on different species, were here combined in the same individual.

VIII. *Direction of the Revolution around the Axis.— Terminology.*

§ 33.

In the revolution round the axis likewise only two different directions are conceivable. They receive names from an oppo-

sition in the dimensions of breadth, right and left. But botanists are not agreed which of the two opposite helices shall be called a right- and which a left-wound helix. According to Linnæus, the Bean winds to the right and the Hop to the left. This definition is arrived at in standing outside the winding, and in tracing the latter from below upwards with the face turned towards it. In this way both the observer and the twining stem examined retain their natural positions. DeCandolle proposed an opposite method. In defining the direction of the winding, he placed himself in the central point, and, on the contrary, called the Hop right- and the Bean left-wound. Most modern authors have followed him, because, as they say, "in every independent object, *right* and *left* can only be determined according to itself, from its own *above* and *below*, *front* and *back*."

§ 34.

The correctness of this reason, however, and the preference herein claimed for the newer terminology, cannot be admitted. According to Kant* the right or left nature of the winding of a spiral is a distinction "which is indeed given in perception, but cannot by any means be clearly conceived, and thus cannot be made comprehensible." We do indeed see, when we hold two oppositely wound helices against each other, that they represent a perfect contrast in their relations to space, and in this way we acquire a conception. But the examination of either singly will not carry us to the same result. All that we attain is a perception in regard to space, and thus terminology would have fully gained its object, if it succeeded in reproducing in us the impression of the direction in space of any helix. Both DeCandolle's and Linnæus's methods fulfil this, but neither of these does any more. I have therefore returned to the terminology of Linnæus, since it is not only the older, but also has the preference over that of DeCandolle on account of greater convenience in use.

§ 35.

Another remark which I have to make on terminology refers to the "æstivatio contorta." Linnæus called flower-buds rolled according to the diagram fig. 1. no. 2, right-wound, in which the

* *Metaphysische Anfangsgründe*, 1787, p. 8.

right border of each leaf covers the left of its neighbour, and those where the opposite case occurs, as in fig. 1. no. 1, left-wound. But the diagram fig. 2 shows that the flower-buds which Linnæus called right-wound owe their origin to a revolution of the individual leaflets to the left, and *vice versâ*. I shall therefore deviate from the terminology of Linnæus in this point, and call buds corresponding to the diagram figs. 1 & 2. no. 1. right-wound, and those agreeing with figs. 1 & 2. no. 2. left-wound.

IX. *Direction of the Revolution around the Axis in reference to the Systematic Divisions of the Vegetable Kingdom.*

§ 36.

The direction in which leaves wind stands, like all the other characters of plants, in a certain relation to the systematic subdivisions of the Vegetable Kingdom. Individuals of the same species behave uniformly in the direction of the heliacally wound leaves, and there are but few exceptions to this. Thus, for instance, specimens of *Medicago littoralis*, Rohdé, occur with the legumes wound to the right and others with them wound to the left.

§ 37.

Whole genera including only uniformly winding species are somewhat rare. When the direction changes within the same genus, the species which have like laws of direction may sometimes be arranged in common subsections of the genus from agreement also in other essential characters. The genus *Allium* furnishes a remarkable proof of this. The *Allia* with left-wound stem-leaves, as *A. acutangulum*, Schrad., *A. Moly*, L., &c., with perhaps the single exception of *A. azureum*, Ledeb., all have a leafless flowering stem, while right-wound stem-leaves occur only in the species with a leafy flowering stem, as *A. oleraceum*, L., *A. sphærocephalum*, L., &c.

§ 38.

Natural families in which winding leaves are frequent, usually include species the leaves of which wind in different directions, but there are certain families in which a perfect agreement exists; the petals of the Ebenaceæ, for instance, are in all cases wound to the left in the bud.

X. *Change of the Direction in the Winding Leaves of the same plant.*

§ 39.

Plants exist in the leaves of which only one direction, to the right or left, is represented, others in which the leaves of one individual exhibit both directions. Such a change of direction in all cases presupposes a difference in the age or situation of the parts of the plant, since two heliacal lines, one turning to the right, the other to the left, form an absolute contrast, mutually exclusive, and so can only occur either on different bodies, that is, in distinct places, or at different epochs of the existence of the same body.

§ 40.

The distinctions which, from the observations I have hitherto made, usually accompany the change of direction, are: 1. The different periods of age of the same leaf; 2. The differentiation of the leaf in reference to point and base; 3. The relative altitude of the insertions of different leaves; 4. The dissimilar lateral insertion, both of the solitary and the verticillate leaves; and 5. The metamorphosis of the leaf.

§ 41.

Since, however, the change of direction depends, in some plants on one, in others on another of these distinctions, there exists a great variety in plants with winding leaves, which is increased moreover by the fact that the lateral direction of the helix, formed by the arrangement of the leaves, may affect in an opposite way the direction of the heliacal winding of the leaves themselves, so that the leaves are wound either in the same, or in the opposite direction, to that of the leaf-spiral. We have now to furnish some instances of the effect of those differences of the position or relative age of the plant on the direction of the heliacal winding.

§ 42.

1. *Different periods of the age of the same Leaf.*

The leaves of the inner circle of the perianth of *Puya cærulea*, Miers, *P. guianensis*, Kl., *Bilbergia zebrina*—Fam. of Brome-

liaceæ; and the petals of *Chrystea speciosa*, Ward et Hartw., *Strophanthus divergens*, Graham—Fam. of Apocynaceæ; *Cyclamen europæum*, L., *Lysimachia punctata*, Wallr.—Fam. of Primulaceæ;—are all wound to the left in the bud, and to the right when the flower blows. The awns of *Arrhenatherum elatum*, M. & K., at first wind slightly to the left below the angle; subsequently, as the seed is maturing, to the right in the same situation. It is probable that similar phænomena will be shown to occur in very many Grasses with winding awns. The appendages of the seed (beak of the carpel?) of *Erodium cicutarium*, L'Hérit., are wound to the left round the carpophore; after separating from it they wind to the right. See Pl. IX. fig. 4. nos. 1 & 2.

§ 43.

2. *Differentiation of the Leaf in reference to Point and Base.*

Alstrœmeria pelegrina—Fam. of Amaryllidaceæ:—stem-leaves winding to the right at the apex and to the left near the petiole. *Avena sativa*, L., and the allied species *Phalaris minor*, L., &c., *Lagurus ovatus*, L.—Fam. of Gramineæ,—and *Xerotes purpurea*, Endl.—Fam. of Juncaceæ:—stem-leaves wound to the left at the points and to the right near the bases. (See fig. 5.) In like manner the awns of many grasses, especially of the genera *Avena*, *Stipa*, *Danthonia*, &c., in which the angle or 'knee' forms the boundary of the two oppositely-directed windings, so that the curvature is to the left above the knee and to the right below it. *Chætobromus Dregeanus*, N. ab E., *Ch. strictus*, N. ab E.: the palea runs out into two teeth above, the awn being fitted in between them; the two teeth wind to the left, the awn to the right below and to the left above. *Strophanthus dichotomus*, D.C.—Fam. of Apocynaceæ:—the left-wound flower-buds are slightly rolled to the left at their points and twisted to the right below. A second change of the direction occurs in the awns of *Macrochloa arenaria*, Koch. Immediately below the knee they wind to the right, then further down to the left, and quite at the bottom again to the right. The very long style of *Protea grandiflora*, Thunb., changes three times to opposite sides, but here the place which the two directions occupy is not determinate, as in the examples above mentioned, for apparently

the right or left direction assumes the uppermost place without any definite order.

A similar change of direction is met with in the tendrils of the *Passifloræ* and the fruit-stalks of many Mosses. In the former the relative situations of the two directions are indeterminate, as in the styles of *Protea grandiflora*; in the latter they are fixed. The winding to the right is here usually uppermost, the winding to the left in the lowest place. But the *Funariceæ* form an exception to this, since their fruit-stalks are wound to the left above and to the right below.

§ 44.

3. *Different relative altitude of insertion of the Leaves.*

Phalaris minor, L., *Ph. cærulescens*, Desf., *Ph. aspera*, Retz., *Ph. canariensis*, L., *Ph. paradoxa*, L.—Fam. of Gramineæ:—the first two leaves succeeding the cotyledon are wound to the left, the succeeding leaves wind to the left at their points and to the right below. In *Avena sativa*, L., and probably the allied species, the first stem-leaf, developed after the cotyledon, winds to the right, the following leaves wind to the left at the point and to the right below, and finally the uppermost stem-leaves, standing in the immediate vicinity of the inflorescence, wind to the left. In *Watsonia fulgens*, Pers., and *W. aletroides*, Ker.,—Fam. of Irideæ—as well as in many plants of the family of the Grasses, *e.g. Anthoxanthum odoratum*, L., *Calamagrostis Epigeios*, L., *Festuca rubra*, Huds., &c., right- and left-wound leaves follow one another apparently without any fixed order.

§ 45.

4. *Unlike lateral insertion of solitary Leaves.*

Dichæa squarrosa, Lindl.—Fam. of Orchideæ,—*Eucalyptus marginata*, Lk., *E. stenophylla*, Lk., *E. micrantha*, D.C.—Fam. of Myrtaceæ:—the distichously alternate leaves are wound in opposite directions on the opposite ranks. *Chrysocoma Linosyris*, L. (see fig. 6), *Galatella linifolia*, D.C., *G. punctata*, D.C. —Fam. of Compositæ,—*Andersonia prostrata*, Sond., *Sprengelia incarnata*- Fam. of Epacrideæ,—*Melaleuca styphelioides*, L.—

Fam. of the Myrtaceæ—and *Acacia micracantha*, Desv. (see fig. 7) —Fam. of the Mimoseæ—have the stem-leaves wound in a helix turning sometimes to the right, sometimes to the left, making the helix by connecting the points of insertion of the leaves on the stem, from below upwards, by the shortest line. In like manner are the distichous or many-ranked verticillately-arranged leaves of *Pinus*, *e. g. P. sylvestris*, L., *P. Pinea*, L., *P. excelsa*, Wall., *P. Mughus*, Scop., &c., determined in the direction of their winding by the direction of the helix which is described by the succession of scales at the base of each fascicle of leaves. The direction of this helix constantly agrees with the direction in which the leaves wind. The reverse occurs in the petals of *Gillenia trifoliata*, Mœnch.—Fam. of Rosaceæ; the *Sileneæ* with three or several styles, *e. g. Silene*, *Lychnis*, *Viscaria*, *Cucubalus*; as also in the species of *Hypericum*, *Geranium*, *Linum* and *Oxalis*, which in their contorted æstivation are wound in a direction contrary to the readily distinguishable spiral of the sepals. Probably the sometimes right-, sometimes left-wound flower-buds of *Statice*, Fam. of Plantagineæ,—*Lysinema*, Fam. of Epacrideæ,—*Cistus*, Fam. of Cistineæ,—*Lavradia ericoides*, A. St. Hil., Fam. of Sauvagesieæ,—*Bombax*, *Helicteres*, Fam. of Sterculiaceæ,—*Hermannia* and *Mahernia*, Fam. of Byttneriaceæ,—*Maronobea globulifera*, L., Fam. of Clusiaceæ,—*Ricinocarpus pinifolia*, Desf., Fam. of Euphorbiaceæ,—and the Malvaceæ, are in like manner dependent on the direction of the forerunning leaf-spiral. There is great difficulty, however, in making out these, and I have not yet succeeded in determining their direction*.

§ 46.

5. *Unlike lateral insertion of verticillate Leaves.*

Chironia frutescens, L., *Ch. grandiflora*, Fam. of Gentianeæ: —stem-leaves in binate whorls. The leaves of the individual whorls are wound in the same directions, the leaves of alternate

* The connection between the direction of the contorted æstivation and the arrangement of the leaves was explained by Alexander Braun so long ago as the year 1838, before the *Naturforscher-Versammlung* at Freiburg, Breisgau. See A. Braun, On regular rotation (or twisting) in the Vegetable Kingdom. *Flora*, 1839, i. 311 *et seq.*

whorls toward opposite sides. *Eucalyptus punctata*, D.C., *E. floribunda*, Hügel, *E. corymbosa*, Sm.—Fam. of Myrtaceæ: —stem-leaves in binate whorls. In each individual whorl the petioles of the opposite leaves are wound towards opposite sides. In the parallel whorls, *i. e.* those which are separated by an intermediate, alternating whorl, leaves wound in like directions are found upon the same sides. The same laws of direction are followed by the stem-leaves of a *Podocarpus*, Fam. of Coniferæ, —a specimen of which, consisting of a branch without flowers, labelled "ex horto Liverpool," exists in the General-Herbarium at Berlin.

§ 47.

6. *Different Metamorphoses of the Leaf.*

Narcissus moschatus, L.:—stem-leaves wound to the left, segments of the perianth towards the right, after flowering. *Æchmea*, *Puya*, *Pitcairnia*, *Billbergia*, *Tillandsia*—Fam. of Bromeliaceæ:—outer perigone wound to the right, the inner to the left, in the bud. *Pavetta indica*, L., *P. caffra*, Thunb. &c.—Fam. of Rubiaceæ:—segments of the perianth wound to the right in the bud, the bursting anthers to the left. *Lychnis coronaria*, Lam., *L. chalcedonica*, L., *L. flos-cuculi*, L., &c.:—petals wound in the bud in the direction contrary to the spiral of the sepals, the style wound to the right. The same relation exists between the petals and the appendages of the carpels in the Geraniaceæ. *Chironia frutescens*, L., *Ch. grandiflora*, Lam.:—stem-leaves on the alternate whorls wound in opposite directions; petals in the bud and dehiscing anthers towards the left. *Arthrostemma Humboldtii*, Fam. of Melastomaceæ:—sepals wound to the left in the bud, the points of the anthers again to the right. *Cistus* and *Helianthemum*: the three larger sepals and the petals wound in opposite directions in the bud. Consequently, were it correct (see § 45.) that the petals of the Cisteæ wind in the bud, in the direction opposed to that of the leaf-spiral, the sepals must be wound in the same direction as the latter.

XI. *Regular Succession of the two Opposite Directions.*

§ 48.

The examples of leaves which wind toward opposite sides, mentioned in § 12, all agree in the circumstance that the direction to the left invariably precedes the subsequently occurring winding towards the right. The leaves with their points and bases wound in opposite directions exhibit a similar condition. With the single exception of *Alstrœmeria pelegrina*, the upper part of the leaf always winds to the left, the lower part to the right. Here therefore the winding to the left likewise precedes the winding to the right, since the upper portion of the convoluted organs is always older than the lower.

§ 49.

The application of the same law may further be shown in organs wound only in one direction, insofar as they are to be regarded, either wholly or in the winding part, as metamorphosed summits or bases of leaves. The summits of leaves, consequently the style, stigmas, anthers, and, above all, the petals in contorted æstivations, which wind at a period when the point only of the leaf has been protruded from the receptacle,—follow the direction toward the left in a vast majority of cases. The blade of the stem-leaves, as a superior region, is most generally, although not quite so frequently, wound to the left, while the sepals and carpels, as metamorphosed forms of the sheathing portion of the leaf, are predominantly wound to the right.

§ 50.

From this it follows that the two directions to the right and left stand in a fixed relation to the different periods of the age of the leaf, which at the same time have their material expression in the upper and lower parts of these organs. The winding to the left belongs to the earlier period of growth, and occurs chiefly in the upper parts of the leaf. The winding to the right follows at a later period, and is connected principally with the upper parts of the leaf. Since the stem, considered in relation to the leaf, represents a structure standing underneath, it is completely in consonance with this law, that, as we find, the

winding stems are turned to the right in about the same proportionate majority of cases, as the petals, at the other pole, are wound to the left in the contorted æstivation.

§ 51.

The relations are somewhat different in the Mosses. As already mentioned, the winding to the right occupies the upper part, that to the left the lower part of the fruit-stalks of Mosses. The winding fruit-stalks of the Mosses are further distinguished from the leaves of Vascular plants by the circumstance that in the latter the upper winding is developed before the lower, while in the former the lower is shown before the upper. Since then the lower winding of the fruit-stalk of the Mosses is directed to the left and the upper to the right, the winding to the left precedes that towards the right here also. The only exception to this occurs in the fruit-stalks of the *Funariæ*, which wind to the right below and to the left above; and in these, therefore, the winding to the right precedes that towards the left.

§ 52.

A similar relation to that just demonstrated between the winding to the left and right and the earlier and later, or upper and lower parts of the leaf, may perhaps be assumed of the windings which derive their determination from the direction of the leaf-spiral, either in the positive or negative sense. We are led to this conjecture by the fact that leaves wound in the direction opposite to the leaf-spiral occur only in the contorted æstivation, and leaves following the direction of the latter, only on circles of stem-leaves, and perhaps the sepals of the family of Cistineæ. The contorted æstivation, on account of the windings, perfectly determinate in their direction in all cases, is especially important, as the principal seat of the upper winding, from the fact that the wound flower-buds take the direction toward the left in a preponderating multitude of cases. It is very probable that a similar import is to be ascribed to it, to that of windings determined in their direction by the leaf-spiral. Under this hypothesis, therefore, we should have to regard the winding contrary to the direction of the leaf-spiral as the upper or earlier, the direction of the leaf-spiral as the lower and later.

XII. *Direction of Winding Leaves in relation to the Direction of the Winding Stem.*

§ 53.

The movement of winding displays itself in two different forms in the stems of plants. There are stems which by their movement twine round a support, and stems which, like winding leaves, complete their movement in freedom without twining round a prop. The remark made above, that stems, as structures situated below, wind predominantly toward the right, and thus form a contrast to the blades of the stem-leaves more frequently winding to the left, holds good, as it remarkably appears, only of winding stems of the former kind. The hitherto little-known winding stems of the latter kind, which occur not unfrequently in the Monocotyledons, wind always in the direction in which the stem-leaves of these plants are wound. Thus we find left-wound flower-stems and stem-leaves in *Eleocharis palustris*, R. Br., Fam. of Cyperaceæ; in all the species of *Xyris*, Fam. of Xyridaceæ, with which I am acquainted; in *Butomus umbellatus*, Fam. of Butomeæ; *Allium acutangulum*, Schrd.; *All. fallax*, Don; *All. ursinum*, L.; *All. Stellerianum*, Willd.; *All. flavescens*, Bess.; *Tulbaghia alliacea*, L.; *T. cepacea*, L., Fam. of Liliaceæ; *Leucojum æstivum*, L., Fam. of Amaryllideæ.—Right-wound flowering-stems and stem-leaves in *Aristidea megapotamica*, Spr., Fam. of Gramineæ; *Pæpalanthus perpusillus*, Kl.; *P. Ottonis*, Kl., Fam. of Eriocauloneæ; *Moræa filiformis*, Thunb., Fam. of Irideæ. Lastly, in *Sisirynchium anceps*, belonging to the family of the Irideæ, the leaves and stems of some specimens wind to the right, those of others to the left, so that in spite of the change of direction occurring in the same species, leaves and stem are always wound toward the same side in the same individual.

XIII. *Individual observations on the Direction of the convolution round the axis, collocated in the order of the Natural Families.*

§ 54.

It is a very remarkable phænomenon that the circularly or helicacally acting forces of nature follow an unchanging, definite

lateral direction in their course. In cosmical nature the planets describe heliacal lines winding to the right in space, by virtue of their circulation from west to east, since this is combined with the advance, in company with the sun, toward a point in the northern hemisphere. In the department of physics we meet with allied phænomena in the circular polarization of light and in the course of electro-magnetic spirals. Organic life exhibits the same laws in the circulation of the blood, in all cases starting from the left side of the animal body, and in the heliacal windings of the shells of Mollusks, which follow a direction determinate for every species. But plants above all give evidence of a wonderful obedience to such laws, in the direction of the spiral vessels, the heliacally winding trunks of trees, winding stems and leaves, and probably also in the circulation of their saps. In regard to the conceptions formed by the intellect, it makes no difference at all in our views of the essential nature of any force working in lateral direction, whether it sets out towards the right or the left. In the rare cases in which the human heart has been placed in the right side instead of the left, it has been demonstrated that this anomaly did not interfere with the vital powers of the body. Nevertheless, Nature, as though dealing here with the most important business, displays the most surprising regularity in this very lateral direction. This apparent contradiction between our ideas and the phænomena of Nature has something in it so remarkable, that a rather detailed account of observations on this particular point may seem desirable. I shall therefore here subjoin my observations on the direction peculiar to winding leaves, singly, in the order of the Natural Families. This collocation will at the same time serve to furnish a summary of the material of which I made use.

§ 55.

Jungermanniaceæ.—*Jungermannia Trichomanis*, Dicks.: dehiscent valves of the fruit wound to the left.

§ 56.

Musci frondosi.—*Cinclidotus fontinaloides*; *Dichelyma falcatum*; *Bartramia pomiformis*, Hedw.; *Tortula ruralis*, Swartz: stem-leaves wound to the right. *Cinclidotus*, *Barbula*, and

Syntrichia: teeth of the capsules, to the right. *Encalypta streptocarpa*, Hedw.; *Barbula rigida*: walls of the capsules, right. *Barbula anomala*, Br. & Sch., furnishes a solitary example of a Moss with the teeth of the capsule winding to the left. From the notice on this plant in the 'Europäischen Laubmoose,' however, "*Peristomii dentes complures ad dextrum* (*i. e.* to the left in the Linnæan sense) *convoluti*," it would appear that instances of the opposite winding also occur, and it would be interesting to discover whether the fruit-stalks also are wound in the contrary direction when the teeth of the capsule are. I have not seen this plant.

§ 57.

Filices.—*Lygodium circinatum*, Swtz.; *L. salicifolium*, Presl; *L. polymorphum*, H. B. & K.: midrib of the frond without definite order, sometimes to the right, sometimes to the left.—Palm* saw two stems of *Ophioglossum japonicum* (with which I am unacquainted) wound round one another toward the right, that is, to the left in our terminology.

§ 58.

Lycopodiaceæ.—*Lycopodium contiguum*, Kl.; *L. mendiocca-num*, Raddi; *L. inundatum*: stem-leaves slightly wound, with prevailing but not exclusive direction toward the right.

§ 59.

Graminaceæ†.

1. *Oryzeæ*.—*Caryochloa chilensis*, Spr.: awns right.

2. *Phalarideæ*.—*Phleum*, *Alopecurus*, and *Beckmannia*: stem-leaves constantly left. *Baldingera arundinacea*, Gaert.; *Holcus lanatus*, L.; *H. mollis*, L.; *Hierochloa borealis*, R. et S.: stem-leaves right. *Anthoxanthum avenaceum*, Retz.: awns right at the lower part.—For the species of *Phalaris* see § 44.

3. *Paniceæ*.—*Setaria verticillata*, Beauv.; *S. viridis*, Beauv.; *S. glauca*, Beauv.; *Pennisetum fasciculatum*, Trin.: stem-leaves

* *Ueber das Winden der Pflanzen*. Stuttgart, 1827, pp. 41, 42.

† See Alex. Braun on the Italian Rye-grass, '*Flora*,' 1834, Jahrg. xvii. Bd. 1. 262, 263, whose attention was already directed to the property of Grass leaves and the awns, of curling in definite directions.

right. Apparently the winding of the leaves is more rare in this section, inclined to a broader development of the leaves.

4. *Stipaceæ.*—*Stipa mongolica*, Turcz.; *Lasiagrostis Calamagrostis*, Lk.; *Aristida megapotamica*, Spr.: stem-leaves right. *Aristida vestita*, Thunb.; *A. chapadensis*, Trin.; *A. Kotschyi*, Hochst.; *A. divaricata*, H. B. W.; *A. Sieberiana*, Trin., &c.: lower paleæ of the flowers right.

5. *Agrostideæ.*—*Polypogon monspeliensis*, Desf.; *P. mexicanus*, Spr.; *Agrostis canina*, L.; *A. vulgaris*, Withering: stem-leaves right. *Apera Spica-venti*, Beauv.: stem-leaves left.

6. *Arundinaceæ.*—*Calamagrostis Halleriana*, D.C.; *C. Langsdorfii*, Trin.; *C. littorea*, D.C.; *Arundo poæformis*, Labil.: stem-leaves right. *Desyeuxia retrofracta*, Kth.; *Lachnagrostis splendens*, Trin.: stem-leaves left. *Calamagrostis sylvatica*, R. Br., and *Desyeuxia eriantha*, H. B. K.: awns right at the lower part. For the stem-leaves of *Calamagrostis Epigeios*, Roth, see § 44.

7. *Chlorideæ.*—*Chloris petræa*, Sw.; *Diplachne poæformis*, Hochst.: stem-leaves right.

8. *Avenaceæ.*—*Aira bottnica*, Wahlenb.; *Avena flavescens*, L.: stem-leaves right. *Trisetum neglectum*, R. & S.; *Tr. Alopecurus*, R. & S.: stem-leaves left. For the doubly wound stem-leaves and awns of the Avenaceæ, as also the doubly wound awns of the Grasses generally, see §§. 42, 43.

9. *Festucaceæ.*—*Poa*, *Bromus*, *Festuca Myuros*, L.: stem-leaves left. *Festuca alpina*, Sut.; *F. arundinacea*, Liljebl.; *F. pratensis*, Huds.; *Bromus cæspitosus*, Host.; *Br. rupestris*, Host.; *Brachypodium ramosum*, R. & S.; *Cynosurus echinatus*, L.; *Briza media*, L.; *Melica pyramidalis*, Lam.: stem-leaves right. As the genera *Bromus* and *Festuca* are so extremely nearly allied, it is important for their distinction that the former are predominantly wound to the left, the latter to the right. For the stem-leaves of *Festuca rubra*, Huds., and *Melica altissima*, see § 44. *Bromus madritensis*, L.; *Br. rubens*, L.; *Br. scaberrimus*, Tenore: awns slightly left. *Bromus confertus*, M. B.; *Br. wolgensis*, Spr.; *Br. patulus*, M. & K.; *Br. lanceolatus*, Roth: awns slightly left.

10. *Hordeaceæ.*—*Lolium*: stem-leaves right. *Triticum*, *Secale*, *Elymus*, *Ægilops*: stem-leaves left. *Elymus Caput-Medusæ*, L.; *E. platantherus*, L.: awns left.

11. *Rottbœlliaceæ.—Lepturus incurvatus*, Trin.: stem-leaves right. *Hemarthria fasciculata*, Kth.: stem-leaves left.

12. *Andropogoneæ.—Tricholæna tonsa*, N. ab E.; *Elionurus argenteus*, N. ab E.: stem-leaves right. *Saccharum cylindricum*: stem-leaves left. *Apluda microstachya*, N. ab E.: stem torn at the apex into filiform strips which wind to the left. *Anthistiria Wightii*, N. ab E.; *A. tremula*, N. ab E.; *A. abyssinica*, Hochst.: awns right at their lower part. *Erianthus contortus*, Elliot: awns left.

§ 60.

Cyperaceæ.—Cyperus reflexus, Vahl; *Cyp. difformis*, L.; *Cyp. auricomus*, Sieb.: stem-leaves right. *Papyrus antiquorum*, Willd.: the narrow glumes enveloping the inflorescence right. *Chrysithrix capensis*, L.; *Fimbristylis torta*, Kth.; *Eleocharis palustris*, R. Br.: stem-leaves left. *Carex hirta*, L.; *C. ampullacea*, Good.; *Rhyncospora alba*, Vahl; *Schœnus nigricans*, L.; *Fimbristylis ferruginea*, Vahl; *F. junciformis*, Kth.; *Androtrichum polycephalum*, Kth.; *Ficinia striata*, Kth.; *Eleocharis glaucescens*, Schult.; *E. palustris*, R. Br.; *E. uniglumis*, Lk.; *Scirpus maritimus*, K.; *Scirpus glaucus*, N. ab E.; *Eriophorum gracile*, Koch; *E. latifolium*, Hoppe: anthers left when dehiscent.

§ 61.

Eriocauloneæ.—Pæpalanthus perpusillus, Kl.; *P. Ottonis*, Kl.: stem-leaves right.

§ 62.

Xylideæ.—Xyris communis, Kth.; *X. subulata*, R. & P.; *X. arescens*, Kth.; *X. strobilifera*, Kth.; *X. metallica*, Kl.: stem-leaves left.

§ 63.

Commelinaceæ.—Tradescantia Lyoni: stem-leaves left; I must remark, however, that I have seen but one specimen of this plant, on the "Pfauen-Insel," near Potsdam.

§ 64.

Juncagineæ.—Scheuchzeria palustris, L. This plant presents individuals with right- and others with left-wound leaves. Leaves of the same specimen wind constantly in the same

direction. Perhaps the direction of the leaf-spiral has an influence here in the direction of the winding, producing, by its difference in different specimens, a corresponding difference in the direction of the winding leaves. I have no exact observations on this point.

Butomaceæ.—*Butomus umbellatus*, L.: stem-leaves left.

§ 65.

Juncaceæ.—*Xerotes mucronata*, R. Br.; *X. æmula*, R. Br.; *X. effusa*, Endl.; *X. suaveolens*, Endl.; *X. rupestris*, Endl.; *X. micrantha*, Endl.; *X. flexifolia*, R. Br.; *X. rigida*, R. Br.; *X. longifolia*, R. Br.: stem-leaves left. *Xerotes umbrosa*, Endl., and two species from Major Mitchell's Expedition, distributed unnamed under the Nos. 542 and 564: stem-leaves right On the doubly-wound leaves of *Xerotes purpurea*, Endl., see § 43. The stem-leaves of some species of *Juncus*, in particular *Juncus compressus*, Jacq., seem to behave like the stem-leaves of *Scheuchzeria*. In many specimens the leaves wind to the left, in others to the right; the right-winding predominate. *Luzula albida*, D.C.; *L. campestris*, D.C.; anthers after dehiscence left. The stigmas of all the species of *Juncus* and *Luzula* with which I am acquainted wind to the left before the flower opens.

§ 65*.

Melanthaceæ.—*Tofieldia calyculata*, Wahlenb.; *Colchicum Szovitsii*, Fisch. et Meyer; *C. autumnale*, L.; *C. variegatum*, Bivon: stem-leaves left. *Merendera caucasica*, M. B.: stem-leaves slightly right.

§ 66.

Liliaceæ.—*Ornithogalum umbellatum*, L.; *O. Gussonii*, Ten.; *O. lanceolatum*, Labill.; *Bulbine annua*, Willd.; *Johnsonia mucronata*, Endl., as well as all the numerous species of the genera *Lilium*, *Eremurus* and *Asphodelus* I have seen: stem-leaves right. *Hyacinthus orientalis*, L.; *Thysanotus proliferus*, Lindl.; *Tulbaghia alliacea*, L.; *T. cepacea*, L.; *Acanthocarpus Preissii*, Lehm.: stem-leaves left. In the genus *Fritillaria* occur species with left- and with right-winding leaves. To the former belong, for example, *F. imperialis*, L.; *F. Meleagris*, L., &c.; to the latter,

F. pyrenaica, L., and *F. montana*, Hoppe. Between many of the oppositely winding species there exists so close an affinity that hybridizing would be most probably successful. It would be interesting to discover the direction in which the leaves of such a hybrid would wind.—For the winding leaves of the *Allia* see § 37. *Gagea minima*, Salisb.: segments of the perianth left during the withering of the flower. *Massonia latifolia*, L.: the filiform bracts of the flowers right.

§ 67.

Smilaceæ.—Streptopus perfoliatus, L.: segments of the perianth left after the flower has opened. *Paris quadrifolia*, L.: the attenuated points of the four stem-leaves, the leaflets of the perigone, both those of the inner and the outer, wind to the left in the bud in the contorted æstivation, and likewise after the flower has opened; finally also the dehiscing anthers and the style, all left.

§ 68.

Hæmadoraceæ.—Conostylis bracteata, Hæmodorum planifolium: stem-leaves right. *Barbacenia tricolor*, Mart.: stem-leaves rolled together like ringlets, without definable order, sometimes left, sometimes right. *Vellozia variabilis*, Mart.: the dehiscing anthers left.

§ 69.

Hypoxideæ.—Hypoxis gracilis, Lehm.; *Curculigo brevifolia*: stem-leaves right.

§ 70.

Irideæ.—Moræa filiformis, Thunb.; *Tritonia lineata*, Ker.; all the species I know of *Ixia* and *Gladiolus*, together with the species of *Iris* with straight, narrow, linear leaves, *e. g. Iris sibirica*, L.; *I. Pallasii*, Goldb.; *Trichonema chloroleucum*, Ker., and several species of *Tritonia* which were temporarily cultivated without names in the Berlin Botanic Garden in 1848: stem-leaves left. In the species of *Iris* with broad, sabre-shaped leaves, *e. g. I. lurida*, Ait., *I. germanica*, L., and *I. Pseud-Acorus*, the attenuated points wind sometimes right and sometimes left. For *Watsonia fulgens*, Pers., and *W. aletroides*, Ker.,

see § 44; for *Sisyrinchium anceps*, § 53. The petals of the species of *Iris* are constantly wound to the left, in the contorted æstivation. *Aristea cyanea*, Ait.; *A. bracteata*, Pers.; *A. capitata*, Gawl.; *A. cærulea*, Vahl; *A. spiralis*, Vahl: petals winding to the left as the flowers wither. The withering flowers of *Iris* exhibit the same twistings, apparently however without definite direction.

§ 71.

Amaryllideæ.—Hitherto I have only met with left-wound stem-leaves in this family. The species examined were: *Leucojum æstivum*, L.; *Sternbergia colchiciflora*, W. K.; *Brunsvigia Josephinæ*, Ker.; a *Cyrtanthus*, the leaf of which is represented in fig. 8; *Zephyranthes candida*, Herb., several species of *Narcissus*, *Gethyllis* and *Alstrœmeria*. For the doubly-wound stem-leaves of *Alstrœmeria peleyrina*, see § 43. *Narcissus moschatus*, L.: petals right soon after the flower opens. *Pancratium patens*, Red.; *P. expansum*, W. Herb.; *P. lobatum*, Kl.: dehiscing anthers right.

§ 72.

Bromeliaceæ.—See § 47 and § 42, for the winding of the outer and inner perianth in the bud, and of the leaves of the inner perigone after the flower is open. We also observe a constant winding towards the left in the style.

§ 73.

Orchideæ.—*Epidendrum macrochilum*, Hook.; *Scaphyglottis violacea*, *Cyrtochilum flavescens*, *Diuris filifolia*, Lindl.: stem-leaves left. *Ornithidium album*, Hook.; *Cymbidium giganteum*; *Disa Zeyheri*, Sond.; *D. tenella*, Sw.: stem-leaves right. For *Dichæa squarrosa*, Lindl., see § 45. *Epidendrum cochleatum*, L.; *Trichopilia tortilis*, Lindl.: perigonial leaflets left, with the exception of the labellum which does not wind. *Orchis hircina*, Scop.: lobes of the labellum, especially the long middle lobes, left. *Cypripedium Calceolus*, L.: the pair of corresponding segments of the outer perigone right. Every one is aware of the half revolution of the germen of many Orchideæ, by which the position of the parts of the flower in relation to the axis of

the inflorescence appears reversed, so that the labellum comes to the front, while in its original position it is turned towards the axis. No definite direction can be detected in this winding; right- and left-wound ovaries succeed one another quite irregularly. It is possible that this revolution is a mere effect of irritability, caused by the effort of the labellum to assume an external position, corresponding to its greater proportionate development.

§ 74.

Aroideæ.—Acorus Calamus, L.: stem-leaves left.

§ 75.

Typhaceæ.—Typha latifolia, L.; *T. angustifolia*, L.; *T. stenophylla*; *Sparganium ramosum*, Huds.: stem-leaves left. *Sparganium natans*, L.: stem-leaves right. The only example I know of a plant winding under water. The winding may be frequently prevented, or its effects rendered imperceptible even by slow flowing of the water. But I observed it very clearly in July 1847, on the heath behind Moabit, near Berlin, in little pools where the undisturbed development of the leaves was favoured by the calm and clearness of the water.

§ 76.

Palmæ.—Maximiliana insignis, Mart.: anthers mostly right-, but occasionally left-wound.

§ 77.

Coniferæ.—For the acicular leaves of the species of *Pinus*, see § 45.—*Podocarpus elongatus*, L'Hérit.; *P. macrophyllus*, Wall.; *P. falcatus*, L'Hérit., and *P. latifolius*, Wall.: stalks of the stem-leaves and lowest part of the blades right.

§ 78.

Casuarineæ.—Casuarina suberosa, Otto and Dietr., and a *Casuarina* from Cuming, discovered in the Philippines and distributed as No. 730: sheath-teeth right. *Casuarina humilis*, Otto and Dietr.; *C. quadrivalvis*, Labill., and *C. suberosa*, Otto and Dietr.: style left.

§ 79.

Salicineæ.—Salix stipularis, Sm.: branches of the stigma right when dried up.

§ 80.

Nyctagineæ.—Bugainvillea spectabilis: withering flowers right. *Pisonia grandis*, R. Br.; a plant which I have never seen myself, but which is represented with right-wound styles in Endlicher's 'Iconographia' (Vindob. 1838).

§ 81.

Gyrocarpeæ.—According to Nees v. Esenbeck,—Wallich, Plantæ Asiaticæ rariores, ii. 68,—the cotyledons are wound helically round the two-leaved plumule: I have had no opportunity of observing for myself. The direction of the winding is unknown.

§ 82.

Santalaceæ.—Thesium ramosum, Hayne: stem-leaves left. The stem-leaves of *Thesium pratense*, Ehrh., and *Th. ebracteatum*, Hayne, are also often wound, but not in any definite direction. *Santalum cognatum*, Miquel: petioles left, not quite $\frac{1}{4}$.

§ 83.

Daphnoideæ.—Passerina pectinata: stem-leaves slightly to the left. The same in *Daphne oleæfolia*, Lam.

§ 84.

Proteaceæ.—Persoonia quinquenervia, Hook.; *Hakea stenocarpa*, R. Br.; *H. latifolia*, Loddig.; *Protea longiflora*, Lam.; *Pr. inflexa*, Willd.; almost all species of *Leucadendrum*, e. g. *L. ascendens*, R. Br.; *L. diversifolium*, R. Br.; *L. tortum*, R. Br.; *L. cuspidatum*, Kl., &c.: stem-leaves left; in *Hakea latifolia*, Loddig., it is the attenuated points of the leaves which wind, in the rest the lower parts of the leaves which run down into an imperfect petiole. *Conospermum capitatum*, R. Br.: the narrow stem-leaves, nearly a foot long, right. *Conospermum teretifolium*, R. Br.: petals in the bud twisted like a cord to the left. For the winding style of *Protea longiflora*, see § 43.

§ 85.

Plumbagineæ.—Armeria, in all the species with which I am acquainted: petals wound to the left in the contorted æstivation. The genus *Armeria* is essentially distinguished by this point from the allied genus *Statice*, in the distichous inflorescence of which right- and left-wound buds alternate regularly. But this law seems only to be manifested clearly in the blue-flowered species of the genus *Statice*. Two red-flowered species, one of which is *St. acicularis*, exhibited a predominance of right-wound flower-buds, with the intermixture of a small number of left-wound.

§ 86.

Compositæ.—Liatris punctata, Hook.; *L. cylindracea*, Mx.; *L. squarrosa*, *L. ciliata*; *Eclopes parallelinervis*, Lessing; *Geropogon glaber*: stem-leaves right. *Cephalophora aromatica*, Schrad.; *Calycadenia villosa*, D.C.; *C. cephalotes*, D.C.; *Metalasia*, R. Br.; *Stœbe*, Less.—almost all the species of these genera—*Perotriche tortilis*, Cass.; *Erythropogon umbellatum*, D.C.; *Elytropappus glandulosus*, Less.; *E. ambiguus*, D.C.; *Disparago ericoides*, Gaertn.; *D. lasiocarpa*, Cass.; *Centaurea depressa*, M. B.: stem-leaves left. For *Galatella* and *Chrysocoma*, see § 45. *Podolepis subulata*, Steetz: points of the membranous leaves of the anthodium not quite ¼ right. *Prenanthes purpurea*, L.: radiant florets thrown back toward the left. R. Brown has directed attention to the windings of the style to the extent of about ¼ of its circumference. The arms of the stigma which stand front and back in reference to the axis of the inflorescence, are thus brought into a lateral position. I have observed this phænomenon, not in all, but in a great multitude of Compositæ, and have never detected a definite law of direction.

§ 87.

Campanulaceæ.—Campanula Loreyi, Pollin.: apex of the calyx left. *Campanula patula*, L.; *C. Rapunculus*, L.; *C. Læfflingii*, Brot.; *C. persicifolia*, L.; *C. cana*, Wall.; *Phyteuma canescens*, W. et K.: dehiscing anthers to the right. *Campanula rapunculoides*, L.; *C. Trachelium*, L.; *C. glomerata*, L.; *C. barbata*,

L.; *C. Loreyi*, Pollin.; *C. Medium*, L.: dehiscing anthers left. The species in which the anthers wind to the same side, exhibit a certain agreement in their habit, which indicates that the two groups which are distinguished from each other by the opposite winding of their anthers may also be separated by other characters. But this requires a more exact knowledge of this large genus than I possess.

§ 88.

Stylideæ.—A slight revolution of the corolla brings the anterior, odd petal into a lateral position. I have only examined one species of this genus, which was cultivated in the Berlin Garden under the name of *Stylidium suffruticosum*. In this the winding of the corollas was without exception directed to the left.

§ 89.

Rubiaceæ.—*Pavetta indica*, L.; *P. Caffra*, Thunb.; *P. lanceolata*, Ecklon; *P. manitensis*, Walpers; *P. longissima*, Kl.; *Ixora Bondhuca*, Rxbrg.; *I. acuminata*, Rxbrg.; *I. parviflora*, Vahl; *I. nigricans*, R. Br.; *Wendlandia coriacea*, Vahl; *Augusta lanceolata*, Pohl; *Randia ferox*, D.C.; *Gardenia latifolia*, Rxbrg.: segments of the flowers right on the contorted æstivation. *Exostemma maynense*, Pœpp.: segments of the flower left in the bud. *Coffea arabica*, L.; *Gardenia latifolia*, Rxbrg.: dehiscing anthers right. *Pavetta* (the above-mentioned species): dehiscing anthers left. The anthers of *Gardenia latifolia*, Rxbrg., and *Pavetta*, consequently follow opposite directions in their winding, while the segments of the flowers of both are turned in the same direction.

§ 90.

Jasmineæ.—*Jasminum officinale*, L.: segments of the flower left, in the contorted æstivation, which however not unfrequently passes over into the imbricated æstivation. *Jasminum hirsutum*, Hoffmsgg.: segments of the flower predominantly right, in the contorted æstivation.

§ 91.

Oleaceæ.—*Fraxinus heterophylla*, Vahl: fruit slightly right during the ripening.

§ 92.

Apocynaceæ.—Segments of the flower wound in the bud, in

certain species right, in others left. Alphonse DeCandolle* has used the direction of the rolled buds in the descriptions of the generic characters. His very accurate statements are made use of in the following summary:—

1. *Parsonsieæ*, Alph. D.C., and *Echiteæ*, Don: seeds with a *coma* above. Segments of the flower left in the bud. The genera *Neriandra*, Alph. D.C., and *Ecdysanthera*, Hook., form exceptions with right-wound segments. Since, however, there has not yet been any possibility of examining their seeds, it is doubtful whether they actually belong here.

2. *Wrightieæ*, Don: seeds with a *coma* below. Segments of the flower right in the bud.

3. *Alstonieæ*, Don: seeds with a *coma* above and below. Direction of the segments of the flower variable. In *Blaberopus*, Alph. D.C., they wind to the right; in *Adenium*, Rœm. et Schult., left. The genus *Alstonia*, R. Br., includes several species with left-wound segments of the flowers, and one other species in which the segments wind to the right,—*Alstonia scholaris*, R. Br.

4. *Plumerieæ*, Alph. D.C.: seeds naked, two separate ovarian segments of the flower wound to the right in the bud in most of the genera. They are wound to the left only in *Kopsia*, Blume; *Odontadenia*, Benth.; *Malouetia*, Alph. D.C.; *Anisolobus*, Alph. D.C., and *Thyrsanthus*, Benth.

5. *Willughbieæ*, Alph. D.C.; *Carisseæ*, Alph. D.C.: seeds naked; ovary simple; segments of the flower right in the bud.

A few other movements of winding of the parts of the flower occur more isolated:—

Thevetia neriifolia, Juss.: funnel-shaped corolla with five-toothed border. In the bud it is weakly folded towards the left, and at the same time wound heliacally in the opposite direction, that is, to the right. *Echites longiflora*, Desf.: the left-rolled buds slightly twisted together to the left above. For *Christya spinosa*, Ward et Harvey; *Strophanthus divergens*, Graham, and *Str. dichotomus*, D.C., see §§ 42, 43. *Parsonsia spiralis*, Wall.; *P. oblonga*, Wall.; *P. Cumingiana*, Alph. D.C.; *P. helicandra*, Hook. et Arn.: filaments left. *Nerium Oleander*, L.: the filiform points of the anthers left.

* DeCandolle, *Prodr. Syst. Natural.* viii. 317–489.

§ 93.

Asclepiadeæ.—Segments of the flower prędominantly left in the bud. I have not observed exceptions to this rule myself. But according to Decaisne*, the segments of the flower are wound to the right in the genera *Secamone*; *Toxocarpus*, W. et A.; *Calostigma* and *Oxypetalum*, R. Br. *Microloma sagittata*, R. Br.: points of the flower-buds twisted to the right. *Pergularia accidens*, Blume; *P. edulis*, E. M.: buds twisted to the left at the points, the unfolded segments of the flower wound to the left. *Diplolepis Menziesii*, R. et S.; *Oxypetalum riparium*, H. B. K.: segments of the flower left after the flower opens. Probably the genus *Pycnoneuron*, Dene., also belongs here, since Decaisne says of it, "Laciniis post anthesin superne dextrorsum contortis," *i. e.* according to our terminology, to the *left*†.

§ 94.

Gentianeæ.—For the winding of the stem-leaves of *Chironia* see § 46. Segments of the corolla of all the Gentianeæ, perhaps with the exception only of *Menyanthes* and *Villarsia*, wound in the bud, and everywhere toward the left. The tubes of the corollas of *Gentiana* are in addition laid in folds towards the right in the bud. *Chironia*, *Erythræa*, *Pleurandra palustris*, Griseb.; *Pl. Krebsii*, Griseb.; *Sabbatia corymbosa*, Ell.: dehiscing anthers to the left. *Lisianthus uliginosa*, Griseb.: style left. *Sabbatia corymbosa*, Griseb.: style right.

§ 95.

Labiatæ.—*Burgsdorfia montana*, Hort. Bot. Berol.: stem-leaves to the left at the base. *Hyssopus lophanthus*, L.; *Lophanthus chinensis*, Benth.: tube of corollas right. The revolution amounts to about $\frac{1}{2}$, so that the lip of the flower is carried to the upper side. Bentham, in his description of the Labiatæ, explains this resupination incorrectly, by a revolution of the flower-stalk‡.

§ 96.

Cordiaceæ.—*Cordia Gerascanthus*, L.; *C. complicata*, Ruiz; *C. alliodora*, Ruiz: segments of the corolla left in the bud.

* D.C. *Prodromus*, *l. c.* 501, 504, 580, 581. † Ibid. p. 582.

‡ Tom. i. Introduction, p. xxiii.

§ 97.

Asperifoliæ.—Pulmonaria maritima, and all the species of *Myosotis* I am acquainted with: segments of the corolla left in the bud. *Trichodesma africanum*, Lehm.; *Tr. indicum*, R. Br.; *Tr. zeylanicum*, R. Br.: points of the anthers wound together towards the left.

§ 98.

Convolvulaceæ.—The corollas of *Convolvulus* and the allied genera are folded to the right and at the same time wound heliacally to the left in the bud. See § 92. for the contrast in *Thevetia neriifolia*, Juss., with which, in other respects, the folding and twisting of the corolla before the opening of the flower exactly agree.

§ 99.

Hydrophylleæ.—Nemophila, all the species as yet known to me, and *Hydrophyllum virginianum*: segments of the corolla right in the bud.

§ 100.

Scrophularineæ.—Pedicularis: the tube of the corolla undergoes a revolution to the left, seldom exceeding $\frac{1}{4}$, during the opening of the flower, whereby the parts of the flower acquire an oblique position. Apparently this revolution commences at that part of the tube which is continued above into the lower lip. This is always most strongly twisted, and it may be clearly detected that the winding of the part of the tube of corolla belonging to it commences independently and alone before the flower opens, and in a comparatively very young condition. Then, as the part of the tube belonging to the upper lip remains in its position, and the part belonging to the lower lip undergoes a curvature to the left, the left side of the lower lip becomes approximated to the upper lip in the same degree as it is removed from it on the right. The result of this is, that the left side of the lower lip becomes more intimately blended with the upper lip than the right, hence the sinus which separates the upper and lower lips on either side is always cut in deeper on the right than on the left. *Pedicularis palustris*, L.; *P. asplenifolia*, Flörke; *P. canadensis*, L.; *P. contorta*, and *P. lanceolata*, Mx., are species

in which all these phænomena are exhibited with especial clearness. Probably traces of them might be discovered in all species. *Anthocercis littorea*: the narrow, lanceolate segments of the corolla to the right after the flower is open.

§ 101.

Acanthaceæ.—*Gendarussa orchioides*, N. ab E.: stem-leaves to the left. *Peristrophe caulopsila*, N. ab E.; *P. Kotschyana*, N. ab E.; *P. speciosa*, N. ab E.; *Hypoestes aristata*, R. Br.; *H. polymorpha*, N. ab E.: tube of corolla right.

§ 102.

Primulaceæ.—*Lysimachia punctata*, Wall.: sepals convoluted to the left at their tops in the bud. *Lysimachia*, *Lubinia*, *Anagallis*, *Cyclamen*, *Trientalis*, and *Samolus littoralis*, R. Br.: segments of corolla left in the bud. *Cyclamen europæum*, L.; *Lysimachia punctata*, Wallr.: segments of the corolla right after the flower is open.

§ 103.

Gesneraceæ.—*Dorcoceras hygrometrica*, Bge.: the walls of the dehiscent capsule left.

§ 104.

Sapotaceæ.—*Mimusops dissecta*, Spr. (Herb. Gen. Berol.): the linear-lanceolate acuminated segments of the flower left, after the flower is open.

§ 105.

Myrsinaceæ.—Segments of the flower frequently wound in the bud, and then constantly towards the left. "Lobis petalisve, æstivatione varia, sæpius sinistrorsum contorta," says Alph. DeCandolle* of this family. According to his observations, *Ardisia Pickeringia*, Torr. & Gray, has right-wound petals. The segments of the calyx are said to wind to the right. I have not investigated this family myself.

* *Prod.* viii. p. 75.

§ 106.

Ægiceraceæ.—"Calyx 5-partitus, lobis sinistrorsum imbricato-convolutis.....Corolla.....lobis æstivatione sinistrorsum imbricato-convolutis." Alph. DeCandolle*. This family also is unknown to me.

§ 107.

Ebenaceæ.—Segments of the flower left, in the bud, in all species.

§ 108.

Epacrideæ.—On the winding of the stem-leaves of *Andersonia prostrata*, Sond., and *Sprengelia incarnata*, see § 45; also, as to the winding of the segments of the flower in this family, and in the family of the Rosaceæ, Caryophylleæ, Hypericineæ, Geraniaceæ, Lineæ, Oxalideæ, Cistineæ, Sauvagesieæ, Malvaceæ, Sterculiaceæ, Byttneriaceæ, Clusiaceæ, and Euphorbiaceæ.

§ 109.

Ericaceæ.—In the great majority of species of the genus *Erica* the segments of the limb of the corolla are wound, and constantly towards the left.

§ 110.

Saxifrageæ.—*Vahlia capensis*, Thunb.: stem-leaves left.

§ 111.

Ranunculaceæ.—*Nigella sativa*, L.; *N. damascena*, L.; *N. hispanica*, L.: style to the left. *Clematis azurea*: appendages of the carpels wound to the right.

§ 112.

Papaveraceæ.—*Platystemon californicum*, Benth.: style of the ripening fruit left.

§ 113.

Mesembryantheæ.—*Mesembryanthemum aureum*, L.: petals convoluted to the left in the bud.

* *Prod.* viii. p. 141.

§ 114.

Sileneæ.—Dianthus diutinus, Kit.; *D. atrorubens*, All.; *D. trifasciculatus*, W. et K. (fig. 9): stem-leaves left. *Dianthus*, *Gypsophila*, *Saponaria*, *Vaccaria*, and generally, apparently, in the *Sileneæ* with only two styles: petals to the left in the bud. The peculiar twisting of the petals in a direction contrary to that of the spiral of the sepals peculiar to the *Sileneæ* with three or five styles, and already spoken of above, does not present itself distinctly in all the species. Thus, for example, I observed in *Lychnis chalcedonica*, L., *Silene Armeria*, L., and many other *Sileneæ*, that the left-wound buds predominate; while, if the petals of every bud were wound contrary to the direction of the spiral of the sepals, right- and left-wound flower-buds ought to exist in equal numbers, since the leaf- and consequently the sepal-spirals of each pair of opposite branches of the inflorescence of this family are wound in contrary directions. Such examples of plants with prevailing but not exclusively left-wound flower-buds form the transition from the *Sileneæ* with petals wound contrary to the direction of the sepal-spiral,—in which, therefore, on account of the antidromy of opposite flower-branches, right- and left-wound flower-buds alternate regularly,—to the two-styled *Sileneæ* with only left-wound buds. *Agrostemma Githago* is a plant in which the sepal-spiral may be particularly easily made out from the imbrication of the teeth of the calyx, and I recommend it for investigation of this point. It shows the law prevailing in the three- or many-styled *Sileneæ* with almost unalterable regularity. *Dianthus deltoides*, L.; *Lychnis coronaria*, Lam.; *L. chalcedonica*, L.; *L. Flos-cuculi*, L.; *Silene repens*, Patrin., &c.: style right.

§ 115.

Frankeniaceæ.—Frankenia campestris, Schauer.; *F. pulverulenta*, L.: tube of calyx right.

§ 116.

Loaseæ.—Loasa lateritia, Gill. et Hook.: capsules mostly wound to the right, more rarely to the left. *Blumenbachia insignis*, Schrad.: capsules right.

§ 117.

Sterculiaceæ.—For *Helicteres*, and its contorted æstivation, see § 16. *Helicteres guazumæfolia*, H. et B.: fruits of the two-flowered cymes probably wound towards opposite sides on account of the antidromy of their leaf-spirals. I have only been able to examine the fruits of this one species, but think the rest would exhibit a similar character.

§ 118.

Xanthoxyleæ.—*Ailanthus glandulosus*, Desf.: fruits wound to the right (fig. 3) at the tips.

§ 119.

Oxalideæ.—Besides the winding of the petals in the bud, already mentioned, I observed a very distinct and constant winding of the stem-leaves to the right, in a species of *Oxalis* which was cultivated in 1848, in Decker's Nurseries at Berlin, under the doubtful name of *Oxalis palmata*.

§ 120.

Onagrarieæ.—(*Œnothereæ*): segments of the corolla left in the bud. *Lopezia*: the upper part of the solitary existing stamen to the right.

§ 121.

Combretaceæ.—*Combretum purpureum*, Vahl: petals in the bud left.

§ 122.

Philadelpheæ.—*Philadelphus coronarius*, L.; *P. Gordonianus*, Lindl.: petals in the bud right. *Philadelphus hirsutus*: petals in the bud left.

§ 123.

Melastomaceæ.—Petals in the bud left, probably in all the Melastomaceæ. For the winding of the sepals and anthers in *Arthrostemma Humboldtii*, see § 47.

§ 124.

Myrtaceæ.—*Callistemon* and *Metrosideros*: stalks of the stem-leaves about $\frac{1}{4}$ towards the left. For the winding of the stem-leaves of *Eucalyptus* and *Melaleuca*, see §§ 45 and 46.

§ 125.

Papilionaceæ.—Dillwynia ericifolia, Sm.; *D. glaberrima*, Sm.; *D. parvifolia*, R. Br.; *D. rudis*, Sbr.; *D. laxiflora*, Benth.; *D. pinea*, Sbr.; *Cœlidium ciliare*, Vogel; *Amphithalea*, Eckl. et Zeyh.: stem-leaves right. *Trifolium circumdatum*, Kze.; *Tr. resupinatum*, L.: the resupination of the flowers of these two plants is produced by a half revolution of the tube of the corolla toward the right. Similar windings of the tube of the corolla are met with also in *Trifolium fragiferum*. But the winding is much slighter here, inconstant in its direction, and amounts scarcely to a quarter of the circumference. *Medicago*: the legumes of most of the species wind to the left. The following have right-wound legumes:—*M. tuberculata*, Willd.; *M. tribuloides*, Lam.; *M. rigidula*, Lam.; *M. striata*. For *Medicago littoralis*, Rohde, see § 36*. *Sesbania ægyptiaca*, Pers.: the very long linear articulated pod left. *Crotalaria retusa*, L.; *Cr. verrucosa*, L.; *Cr. ovalis*, Pursh; *Cr. quinquefolia*, L.; *Cr. carinata*, Steud.: the dried-up style right. The twisted styles of some species of *Lathyrus*, *e. g. L. rotundifolius*, Willd., and of *Phaseolus*, follow the same direction. The revolution, however, begins here in the bud, and is imparted to the keel tightly enclosing the style, the former thus likewise acquiring an heliacal winding. *Petalostemon candidum*, Mx.: drying-up style wound in many flowers to the right, in others to the left. *Dalea brachyptera*, Kunze: style slightly left. For the revolution of the phyllodia in *Acacia micracantha*, Desf., Fam. of *Mimoseæ*, see § 45.

XIV. *Cause of the Curvature of Wound Leaves.*

§ 126.

The curvature of the winding leaf depends either on an unequal tension of its margin in relation to the axis, or on an inequality of length of its two surfaces. The specific gravity, which otherwise is certainly to be enumerated among the causes of the curvature of the leaf, comes but little or not at all into

* See also A. Braun on "Regular Revolutions in the Vegetable Kingdom," *Flora*, 1839, i. 313, in which the heliacal winding of the legumes of the species of *Medicago* is described correctly according to DeCandolle's method of defining it.

account in the winding leaf. For since the weight always draws downward, if it were this that compelled the winding leaf to curve, the latter must, in every half revolution, according as it turned this or that side downward, curve, alternately, at one time to this, at another to that side. It must consequently —see § 31.—turn sometimes one, sometimes the other side to the interior of the helix. But it is just one peculiarity of winding leaves, that they always turn one side to the interior of the helix, no matter how many revolutions the leaf may make. The cause of the curvature can only be sought therefore in the leaf itself, and not in any one-sided force acting upon it from without.

§ 127.

The unequal tension of the margins of a leaf in relation to the axis, and the parts lying next to it, is produced by the revolution around the axis. It lies in the nature of the curve, as a bent line, that the heliacally wound lateral parts of a leaf with a straight axis must have passed over a longer course, and therefore must be longer, than this axis itself, which travels through about the same distance by a straight path. If a leaf winding round its straight axis is unrolled, the margins are thrown into waves and folds, and thus present clearly to the eye the overplus of longitudinal development which was expended in the formation of the heliacal curve. But such forms of the leaf are comparatively rare. In the great majority of leaves the borders and axis exhibit a perfect uniform longitudinal development, and no obstacle is offered to their parts being spread out in one plane. Hence it is clear, that, when such a normally formed leaf becomes affected by revolution of its axis, its first effort must be directed to supply the want of predominant longitudinal development by elongation of the lateral part of the leaf. The extensibility of vegetable fibre is certainly capable of this up to a certain point. Vegetable fibre is, however, at the same time elastic, and thus the force which expands it is met at once by another force, which strives to draw it back again into its former dimensions. Only a part of this form can be taken off by the curvature of the axis, since the two forces do not act in diametrical opposition, but obliquely against each other. Another part of the force

remains over, and draws the leaf downward from the point where the revolution of the axis takes place. The results are various, according as the leaf is strong enough to oppose a resistance to the pressure burdening it, or not. In the former case the revolution of the axis is limited to the degree admitted by the extensibility of the fibre, which is so slight that the movement of winding possible under such conditions will remain almost invisible to our eyes. But if the leaf gives, and curves, there arises, as we have seen above, § 30, from the combination of revolution of the axis and curvature, a new movement, which is very essentially distinguished from mere revolution of the axis, insomuch that now all parts of the leaf, its axis included, take share in the heliacal winding around an ideal axis lying outside the substance of the leaf. The contrast which appears between axis and margins in a leaf wound round its own axis, is completely removed, and it no longer requires a predominating longitudinal development of the lateral parts of the leaf to render the heliacal winding possible. In this way the obstacles opposed to revolution of the axis are removed by the curvature of the leaf, after the revolution of the leaf having itself previously produced the curvature. The two movements then act as reciprocal causes, and the result is that revolution of the axis and curvature of the leaf are mostly combined; winding leaves not curled are, on the contrary, very rare.

§ 128.

At the same time it is true, that in the curled winding leaf, two other contrasts, likewise accompanied by an unequal tension in the substance of the leaf, present themselves in the place of the contrast between the axis and margins of the leaf, removed by the curvature. Under supposed equal longitudinal development of both surfaces of the leaf, in the first place, the surface turned outwards must be rendered more tense, since it describes a larger arc, than the surface turned to the interior of the helix, and this in the greater proportion as the leaf is thicker. Secondly, from mechanical causes which it would occupy too much space to discuss here, one margin of the leaf,—namely in left-wound leaves with the upper face turned inwards, and in right-wound leaves with the lower surface turned inwards, the right

margin—as seen from below; and in left-wound leaves with the lower face turned inwards, and also in right-wound leaves with the upper face inwards, the left margin—must be rendered more tense than the other, and this the more, the broader the leaf is in proportion to its length. But the leaves which, as we here presuppose, are curved by the pressure arising from the revolution of the axis, cannot, for that very reason, be very broad or very thick, since otherwise they would not give to the certainly very slight pressure acting upon them. The very slight breadth, in proportion to the length, is, as already remarked, a characteristic peculiarity of all winding leaves. The unequal tension of the surfaces and borders of the leaf caused by curled wound movement, is consequently really so inconsiderable, that it is doubtless mostly compensated by the extensibility of vegetable tissue.

§ 129.

The unequal length of the two surfaces, and the curvature of the leaf caused by this, is the effect of a hygroscopic difference of these surfaces, on account of which their relative lengths alter in the drying-up of the leaf: whether this happens through an elongation or shortening of one of the two faces, I must leave undecided, from the want of accurate observations. This hygroscopic curvature of the leaf acquires especial importance in regard to the revolution of the axis, when this requires a curvature of the leaf to bring it to light, not being strong enough in itself to produce this. The heliacal winding of the leaf is thus first made possible through the addition of the hygroscopic curvature to the revolution of the axis. Since the former, however, depends upon the desiccation of the leaves, only making its appearance towards the end of the life of the plant, the revolution of the axis in this case makes its first appearance in the latest stages of growth as the last expression of an expiring vitality.

§ 130.

Such winding leaf-structures, which are very remarkable, like the awns of the Grasses, the appendages of the carpels of the *Geraniea*, the carpels of *Dorcoceras hygrometrica*, Bunge, &c., possess the property of recovering the originally equal length of

their two surfaces, in contact with moisture. The curvature is thus removed, and in the same proportion as the leaf stretches itself straight, the heliacal winding only possible under the hypothesis of a certain degree of curvature, is unrolled. As soon as the leaf dries and again curls, under the influence of the again increasing difference of length of its two surfaces, the heliacal winding is restored. The whole of this movement depends therefore upon a play of mere mechanical forms, totally distinct from that originally causing the revolution of the axis. They nevertheless have been confounded in many cases. The heliacal winding of awns, the fruit-stalks of Mosses, &c., has been generally looked upon as an effect of their hygroscopic nature, without separating the two different movements contained in it, and the mechanical explanation of the whole process following as a consequence of this view, may have contributed to have drawn away the attention of botanists from the striking physiological phænomenon of revolution of the axis, which is exhibited so clearly in these very structures.

XV. *Causes of the Revolution of the Axis.*

§ 131.

To cause the revolution of the axis, we must imagine a force circulating in a direction perpendicular to the longitudinal direction of growth. It is an immediate revelation of the vital force acting in the interior of the plant, and therefore stands in the closest connexion with the growth as its regular expression. Such a connexion may be detected in some cases by the circumstance, that in the plants mentioned in § 45, the lateral direction in which solitary leaves follow one another in a spiral line, acts in determining the direction of the heliacal winding of the leaf, in other cases it becomes observable in the remarkable inverse proportion between transverse growth and revolution of the axis, through which leaves, in which the growth in breadth has become developed in the angle-nerved venation, exhibit no revolution of the axis, while parallel-nerved leaves in which growth in breadth is deficient, develope that force rotating at right angles to the direction of longitudinal growth, requisite for the revolution of the axis. That this inverse proportion between growth in breadth and revolution actually does exist, and that the parallel-nerved leaves do not exclusively wind, merely

because the usually narrow form opposes the least resistance to the rotating force, perhaps present as in other leaves and only restrained in its effects, is testified by the occurrence of angle-nerved leaves of very long and narrow shape, which, nevertheless, do not wind. So far as regards length and breadth of their parts, these stand in exact agreement with parallel-nerved leaves; indeed the lobes and pinnæ into which they frequently divide are sometimes much finer and more delicate than those of winding parallel-nerved leaves. If, therefore, the forces moving the parallel-nerved leaves were active in these, they ought to exhibit the same effect, and it should produce an heliacal winding of the angle-nerved leaves in a determinate direction. But we do not see this;—proof, consequently, that the angle-nerved leaves are devoid of the rotating force, and that the cause of the absence of revolution of the axis from them does not arise from their merely opposing a greater resistance than the parallel-nerved leaves to a rotating force existing in them. Hence latitudinal growth of the leaf and rotation of the axis are really mutually exclusive. When the former is developed, the latter is wanting, and so it seems to follow from this that one and the same force lies at the foundation of both, manifesting itself either in the transversely directed activity of growth, or, when this is absent, in a lateral movement of the leaf.

§ 132.

While attention was paid merely to winding stems, it was possible to suppose the object of this motion to be that of obtaining attachment to outward objects. We are now aware that a great proportion of winding stems, and winding leaves in general, never coil round a support nor contribute to the fixing of a plant. The latter, therefore, appears to be merely an isolated application of the movement of winding in the œconomy of nature, and we must confess that we are totally ignorant of its peculiar relation to the vital purposes of the individual, or the propagation of the species. This movement is, at the same time, the most frequent of all those detected in the outward organs of plants. The number of plants with winding stems alone, particularly if we include the winding flowering stem of the Monocotyledons and the winding fruit-stalks of the

Mosses, is very considerable. Still larger is the number of the plants with winding leaves enumerated in §§ 55–125. And it must not be forgotten that, according to § 127, there must be movements of rotation which escape notice on account of their slight degree; as indeed, for example, the rotation of the individual leaflets which causes the contorted æstivation is so slight, that it would be wholly concealed were not its traces preserved by the regular overlapping of the margins. In the face of such considerations, the character of external fixedness, which it has hitherto been customary to connect with the conception of a plant, vanishes, and we rather arrive at the conviction that plants, too, possess, in the rotation of the axis, a motion peculiar to them, which reveals itself everywhere that the moving force has not been already exhausted in latitudinal growth, and there found a different expression proportionate to it.

EXPLANATION OF PLATE IX.

Figs. 1 & 2. Each of these figures represent horizontal sections of two pentaphyllous buds rolled to opposite sides.

Fig. 2. is intended to render clear the direction followed in the rotation. If the line *a b* is to be removed, by a rotation round the point *x*, the point of section of the axis of the leaf, into the situation marked by the line *c d*, this takes place by a rotation which is continued to things standing outside the rotation, as the arrows indicate, in No. 1. from left to right, in No. 2. from right to left. The comparison of the two figures 1 & 2, shows us that the æstivation fig. 1. No. 1. is produced by the former movement, the æstivation fig. 1. No. 2. by the latter. Therefore, in logical application of the Linnæan terminology of the æstivation, we call the arrangement fig. 1. No. 1. right-wound, that of fig. 1. No. 2. left-wound.

Fig. 3. Fruit of *Ailanthus glandulosa*, L., wound to the right at the summit.

Fig. 4. No. 1. Fruit of *Erodium Cicutarium*, L., on an enlarged scale. The appendages of the carpels are wound to the left round the carpophore. No. 2. A carpel separated from the carpophore, also magnified; the appendages wind to the right.

Fig. 5. Leaf of an *Avena*, which is wound to the right below, and to the left above.

Fig. 6. Branch of *Chrysocoma Linosyris*, L. Leaves wound to the right in agreement with the direction of the leaf-spiral.

Fig. 7. Branch of *Acacia micracantha*, Desv. Phyllodia wound to the left in correspondence with the direction of the leaf-spiral.

Fig. 8. A left-wound and at the same time strongly curved leaf of *Chrysanthus angustifolia*.

Fig. 9. Branch of *Dianthus trifasciatus*, W. & K., with left-wound leaves.

[A. H.]

ARTICLE X.

On the Development of the Ascidians. By A. KROHN.

[From Müller's *Archiv*, 1852–1853.]

IN setting forth the results of my observations on the development of the Ascidians, it is nowise my intention to lay before the reader a connected account of all the appearances which they present. Considering the earlier works in this department, I shall endeavour to exhibit only the most important steps, and in connexion therewith, as occasion may serve, to consider sometimes one, sometimes another organ, whose mode of development may possess a special interest. I will premise here that the facts I am about to communicate all relate to the development of the *Phallusia mammillata* of Cuvier, and have been obtained by the employment of artificial fecundation *. By this method I have succeeded in following out their progress step by step for three months, until the young Ascidians had attained the size of a line or more. I commence with the unfecundated ovum, inasmuch as its structure is distinguished by many important peculiarities.

1. *Unfecundated ovum.*—The fully formed ova which fill the oviduct consist, most externally, of a villous investment, within which is the proper vitellary membrane. Under the vitellary membrane there lies a glassy layer, in which roundish green structures of a peculiar kind are imbedded, and which surrounds the colourless yelk. The germinal vesicle and spot, both of which are still readily distinguishable in the ovarian ova, are already wanting †.

The investing membrane is thin, and beset superficially by

* The first successfully conducted attempts to fecundate the ova of the *Phallusiæ* were made by Von Baer.

† The same structure is exhibited by the unfecundated ova of the *Phallusiæ* in general, as well as by those of the genus *Clavelina*.

numerous short, blunt-pointed processes. Each villus consists of an aggregation of round, transparent, vesicles or cells, without nuclei.

The glassy layer which lies upon the yelk is altogether homogeneous, but is otherwise remarkable from the first-mentioned structures which are imbedded in it*. Each of these bodies consists of densely aggregated vesicles or cells. We find these structures sometimes solitary, sometimes united into groups of different forms and sizes, in the glassy layer. The latter is, however, nothing else than the primitive rudiment of the mantle, which is already present in the unfecundated ovum of the future *Phallusiæ*. The green structures, which persist unchanged during the whole of larval life, change, after metamorphosis has taken place into the granules, which are contained in abundance in the mantle of the adult animal. This layer has already been recognized by Milne-Edwards (Obs. sur les Ascid. composées des Côtes de la Manche, p. 26. pl. 4. fig. 4) in the ova of *Amouroucium proliferum*, and has been quite justly interpreted to be the future test (Mantelschicht), as the following passage especially shows, p. 36 :—"La couche tegumentaire (*i. e.* the test) est dans le principe la couche gélatineuse (glassy layer) qui dans l'œuf revêt en dehors la masse vitelline." According to this, however, Kölliker's view (Annales d. Sc. Nat. 1846, t. v. p. 218), that the test in *Amouroucium Nordmanni* and *Aplidium gibbulosum*, arises only after the cleavage of the yelk, is confuted; and I cannot doubt that it is this layer, which has been regarded by Van Beneden (Mém. sur l'Embryogénie, &c., des Ascidies, in the Mém. de l'Acad. Roy. de Bruxelles, t. xx. p. 37) as the albumen of the egg, although Milne-Edwards expressly draws attention to the possibility of falling into this error.

2. *Yelk Cleavage and Embryo.*—Without doubt the ova, as Cuvier already supposed, and Von Baer has endeavoured to demonstrate with more conclusive arguments, are fecundated in the so-called cloaca, into which the seminal canal and the ovi-

* The remarkable green or yellowish green colour of the ovarium and of the oviduct, in many *Phallusiæ*, arises entirely from these green structures. When the latter are colourless, as in *Clavelina* for example, the parts in question are without colour.

duct open, close by one another. Since, however, in the *Phallusiæ*, we never meet in this cavity with ova whose development has commenced, as is commonly the case in the compound Ascidians, perhaps nothing is more probable than that the ova are cast forth soon after fecundation, and that their development begins first, external to the parent.

The cleavage of the yelk commences, about two or three hours after the semen has been brought into contact with the ova. It proceeds for the first stages, at least, in a very regular progression. I believe I have made out with tolerable certainty that every cleavage mass, after the completion of its division, is surrounded by an excessively delicate membrane. On the addition of water impregnated with acetic acid, we see this investment gradually raised up from the vitelline contents, which contract into a smaller space, as an independent membrane. As regards, however, the clear vesicular nuclei within the cleavage masses, I believe I have arrived at the result, that they disappear when a new division impends, and only after this has come to an end do they reappear again, newly formed. In their place there may be observed, in any yelk-mass about to divide, a very peculiar arrangement of the vitelline molecules. The latter are in fact disposed in thick striæ, which radiating from the centre, are directed on all sides towards the lighter periphery of the mass, and seem to spread from two centres of irradiation. When, after the completion of division, the nuclei appear within the new cleavage masses, the radiate striation has also disappeared, and the yelk-granules are seen, lying close to one another in the masses, without any definite arrangement. All these appearances agree, however, with that later view of the cleavage process, which was first taken by Riechert (Müll. *Archiv*, 1846, p. 196).

The glassy layer upon the yelk, which we have just described as the original rudiment of the test present in the unfecundated ovum, takes not the smallest share in these thorough changes of the yelk; it remains, without undergoing any alteration, closely apposed to the vitelline membrane.

Before the expiration of the first four-and-twenty hours after fecundation, we find in most ova that the embryo has assumed its well-known cercarian form, with a more or less developed

tail. It is invested by the test which contains the, as yet wholly unchanged, green structures, and is separated from the vitellary membrane by a space filled with fluid. The substance of the body and of the tail consists of cells; at least the latter are clearly distinguishable on the surface of these parts. The cells are polygonal, contain granules, and in addition a central nucleus; the axis of the tail is composed of larger rectangular cells, simply disposed in series, one behind the other, and also provided with a central nucleus, thereby attaining a transversely striated or articulated appearance *.

There are various views as to the mode in which the tail is formed. According to Milne-Edwards the peripheral portion of the embryo, as it were in one piece, becomes constricted off from the body. Kölliker follows this opinion when he states that the tail grows out, not in the manner of a process, but, as a determinate portion of the blastema, becomes separate all at once in its whole length from the body. According to Van Beneden, on the other hand, the tail buds forth as a short process, which elongates by degrees. I can but confirm this last opinion. In fact, according to my observations, the tail appears in the younger embryos, very short and thick in relation to the body, although it is already slightly curved. Afterwards it becomes continually longer and more slender, embracing the body in a continually larger arc, until at last it has grown up to such an extent that its terminal portion enfolds the anterior part of the body of the embryo.

A short time before the completion of the development of the larva, the tail undergoes remarkable changes. The axis becomes hollowed out, its whole cellular substance disappearing into a canal. This excavating process, which is accompanied by a contemporaneous liquefaction of the cell-contents, appears always to proceed from the two walls which are in contact with one another, of every pair of cells, and indeed in many places at the same time, extending further and further, until at last, by the flowing into one another of the separate cavities, the canal in question is formed through the whole length of the axis. In

* This composition of the axis of the tail of large rectangular cells was first demonstrated by Kölliker in the embryos of *Amouroucium Nordmanni* and *Aplidium* (*l. c.* p. 221. fig. 43).

the meanwhile, however, the superficial layer of the axis of the tail, which is composed of smaller cells, appears to have become metamorphosed into a muscular layer consisting of longitudinal fibres, by whose energy those active movements of the tail exhibited by the young larvæ after birth are performed. At present these movements are manifested only by the occasional twitches of the tail, which become more and more frequent in the last period of larval development. In consequence of these twitchings, the vitelline membrane eventually becomes torn, and thus, towards about the thirtieth hour after fecundation, the larva escapes.

One point must not escape notice; with regard to those two dark pigment spots which have been observed on the back of the larval embryos, but which have been, as it seems to me, too hastily taken for eyes. At first we see only a single pigment spot exactly in the middle line of the back. Behind this and more laterally a second, larger one, soon becomes visible (Pl. XII. B. fig. 1. *e*). I have never succeeded in discovering any refractive medium in these pigment spots; but I could, as little, satisfactorily interpret the optical expression of the immediate neighbourhood of these spots, which I have endeavoured to reproduce truly in the figure just cited. This much is certain, that both pigment spots, which in the larva remain always separate from one another (see fig. 2), approach quite closely in the course of metamorphosis and, during the development of the young Ascidian, continue to appear for a long time as an apparently single mass, lying close below the nervous ganglion. In the end, however, this mass breaks up into the two original portions, or even into many pieces, and so passes into the current of the blood, in which they may be seen driven up and down for a time, until at last they are wholly dissolved and disappear. This long continuance of the pigment spots, extending far beyond larval life, appears to me not to be in accordance with the function ascribed to them. For the present, therefore, their true import remains doubtful.

3. *Larva* (see fig. 2).—The body of the hatched larvæ is elongated, has two slightly convex, lateral surfaces and is provided at its anterior extremity with three very short processes, as it would seem excavated into suckers. Two of these lie

higher and laterally opposite to one another; the third, which springs from the middle of the anterior part of the body, is more inferior. By means of these prolongations, which are seen as conical processes even in the embryos (fig. 1. *c*, *c*), the larva attaches itself to some appropriate place in order to go through its metamorphoses. These processes, first seen by Milne-Edwards, and first justly interpreted by him, and whose existence has been confirmed by Kölliker, have been, it would seem, quite overlooked by Van Beneden.

With regard to the portion of the test which invests the tail, it may be stated here, that it terminates in a fin-like, expanded, probably horizontal appendage. The true composition of this appendage is, at first, the more difficult to perceive, as it can rarely be got under the microscope with its whole breadth at once. Therefore, it seems to me, as if the flabelliform process, into which, according to Van Beneden, the test of the tail in the larvæ of *Ascid. ampulloides* (*l. c.* pl. 2) runs out, were a similar appendage, only more strongly developed, and seen from the edge.

4. *Metamorphosis and Development.*—The changes which the tail undergoes, immediately after the attachment of the larva, have been already described by Milne-Edwards in a manner, in the main, in accordance with nature. According to this observer, the contractile central portion or axis of the tail becomes gradually retracted from its investment and passes at last into the body of the larva, so that the investment remains behind, as an empty sheath, which subsequently falls off. Milne-Edwards' investigations give no account of the further fate of the retracted axis.

According to what I have seen, the loosening and retraction of the axis of the tail, which, as we saw, sinks deep into the body of the larva, are only the forerunners of the retrogressive metamorphosis which it soon undergoes. Immediately after its retraction, we find the tail still in good preservation in the posterior division of the now enlarged body. Here it lies rolled up spirally into a coil, which may be pressed out of the body or unrolled by the use of carefully increased compression. Whilst the development of the young Ascidian commences, the coil breaks up first into many closely appressed lobes, and now

withers away by degrees in such a manner that the lobes become smaller and fewer, until they are but minute remnants. In the end these also disappear. When the coil begins to diminish, it occupies, as before, the whole posterior division of the body of the developing Ascidian; but subsequently, when it has become visibly smaller, it lies more on the left side near the œsophagus (Pl. XII. B. fig. 3).

From what has been said then, it results, that Van Beneden has not rightly comprehended the appearances during the extrication of the tail from its investment, since he considers this act, which for the rest his figures depict very well, to depend upon an absorption of the tail. Had Van Beneden recognized all the phases of the retrogressive metamorphosis of the tail, he could not long have remained in doubt as to the true nature of the undefined organ (*l. c.* pl. 3. figs. 11 & 12 *e*) met with in the posterior part of the body of *Ascidia ampulloides* during the first periods of development. He would have at once seen it to be the coiled-up and already lobulated tail.

Very soon after the tail has been withdrawn into the body, and the latter has thence even to some extent increased in size, the three processes of attachment of the larva disappear, while in the meanwhile the mantle of the developing animal is fastened to the ground by its whole lower surface. From the mass of the body, and indeed from the midst of the abdominal surface, three processes of another nature now grow forth, and penetrating deeper and deeper into the mantle, attain its surface. These hollow processes are the first indications of that dichotomously branched vascular system, with distinct walls, which penetrates the mantle of all *Phallusiæ**. These processes are soon seen to become longer and to divide dichotomously into the first branches, whose extremities appear clavate; the dichotomous branching goes on further and further, and the terminal branches

* According to Kölliker's more exact investigations (*l. c.*), this vascular system consists everywhere of double vessels, which running close together ramify correspondingly, and accompany one another to the very finest terminal ramifications, when a mutual anastomosis takes place. According to my observations, this anastomosis occurs in such a manner that the terminal twigs of the two vessels bend round into one another like a loop. All these observations are also, as we shall see, perfectly confirmed by the study of development.

are always found enlarged in the mode described. In young developing Ascidians which have fixed themselves normally, that is, by their whole under surface, we see subsequently, when the vessels of the test have branched out extensively, that all the branches and twigs extend perpendicularly and radially, on all sides, towards the circumference of the mantle. In those individuals, on the other hand, which have been unable to find any, or no convenient, place for fixing themselves, while still larvæ, but whose development nevertheless goes on*, the original vessels of the test, namely the three above-mentioned processes, as well as their subsequent ramifications, take the most various directions, curving downwards for the most part. It would seem, therefore, as though a speedy termination were put to the further ramification by the above-mentioned unfavourable circumstances; such individuals probably die prematurely.

It is, however, so much the easier to mistake the true nature of the vessels of the test, during the early stages, since even when the heart has appeared and the circulation has become established, we see not the slightest trace of any current of blood in them. In addition, the mantle is so transparent that its contours are easily overlooked, and the idea may readily arise, that the much more sharply defined vessels extend beyond its boundaries, whereas they are invested by it. It is therefore difficult, at first, to avoid considering the vessels of the test as stolons or runners, by the aid of which the young Ascidian seeks to fix itself more and more strongly to its residence. This view has the greater plausibility because many Ascidians (*Cynthia papillata* for example) do, in fact, attach themselves to foreign bodies by means of branched stolons; however, the establishment of the circulation in these vessels of the test at once releases us from this error. At first one sees nothing but a column of blood containing merely a few granules, irregularly oscillating. Afterwards, when the ramifications have extended, the blood is more rich in granules and the circulation goes on more rapidly; the oscillation is converted

* A yet more striking example how little the course of development allows itself to be arrested, is presented by certain larvæ which have been unable to burst their envelopes, but whose metamorphosis has nevertheless commenced, as we see by the coiled tail and the commencing formation of the vessels of the test.

into a regular current; at the same time the, originally, quite simple main trunks and branches have become double, whilst their globularly enlarged, terminal twigs, directed towards the periphery of the mantle, are still simple tubes. In the larger vessels, which accompany one another and branch out in common, just as in the adult animal, the blood now streams in two opposite directions, in the one vessel towards the periphery, in the other towards the heart. Shortly before the division of the last branches into the terminal ramuscules, we see these two streams pass into one another by a loop; on the other hand, in the terminal branches no continuous current of the blood is as yet to be observed; the blood-corpuscles indeed penetrate into them, but they frequently stagnate and sometimes become excessively accumulated. They are only occasionally seen to enter the current and return in one or other of the streams we have mentioned. All this continues until the doubling has extended as far as the terminal twigs. The cause of the two opposite currents is readily discovered, inasmuch as observation shows that each of the double vessels opens into opposite ends of the heart. Since, furthermore, the heart, even soon after its appearance, pulsates periodically in two opposite directions, at every change, we see the current of blood in each vessel reversed.

Van Beneden has described processes very analogous to the rudiments of the vessels of the test, growing forth in the *Ascidia ampulloides*, soon after the retraction of the tail; after a short existence, however, they disappear. If these last processes are identical with the vessels of the test of the developing *Phallusiæ*, the latter statement contradicts the observations communicated above. *Ascidia ampulloides* is very probably a *Cynthia*. The cartilaginous test, the plaited respiratory sac, and the double reproductive organs, arranged exactly as in the *Cynthia*, speak for this view. In the mantle of the *Cynthiæ*, so far as I know, no vessels have as yet been demonstrated. If they be absent, then the processes indicated by Van Beneden must have some other import; if they be present, the statement that the processes soon disappear is probably erroneous*.

* The budding vessels of the test will not easily be confounded with the puzzling diverticula of the test, which, Proteus-like, sometimes protrude, sometimes are again retracted and disappear wholly, observed by Milne-Edwards

With respect to the first stages of development, I have not obtained all the information I desired, on account of the many difficulties in the way of a satisfactory examination. Nevertheless I will not hesitate to communicate, in a condensed form, the observations which belong here, imperfect as they may be. It will be observed that as regards many points, they harmonize with the views of Van Beneden.

Soon after the three hollow processes, the rudiments of the future vessels of the test, have appeared, we distinguish in the body, besides those parts which belonged to the larva, viz. the two pigment spots, now closely approximated, and the coiled tail, a cavity which represents the future respiratory or gill-sac. Immediately behind this appears the first indication of the alimentary canal, which appears in the form of a canal, everywhere of even diameter and bent round into the form of a loop. The whole posterior division of the body is filled by the coil of the tail.

Subsequently one may observe on the dorsal surface, on the second layer of the body, which lies under the mantle and is clearly distinguished, three apertures, over which the mantle, still imperforate, passes. The one lies exactly in the middle at the anterior extremity of the body, the two others are altogether lateral and diametrically opposite to one another, in the middle portion of the body. The anterior, somewhat larger, corresponds with the future ingestive or respiratory aperture; the two posterior are intended to take the place of the future cloacal aperture, which arises, at a much later period, by their coalescence. At this time the nervous ganglion also has become developed, and may be readily distinguished as an elongated structure in the middle of the dorsal surface and close above the two pigment spots. Near it we see the first indications of the future interwoven muscular cords of the body; the abdominal furrow is already indicated; the nutritive canal has become further developed; it lies now, for the most part, above the respiratory sac and describes a curve, commencing at the bottom of the latter and passing round to the immediate neighbourhood of the left excretory aperture. Three divisions may

during the development of *Amouroucium proliferum*, and which he has fully described.

be distinguished in it, the œsophagus opening into the respiratory sac, the stomach, and the intestine.

Soon after this there appear in the wall of the respiratory sac the first respiratory or gill-clefts (*stigmates branchiaux*, M. Edw.), in the form of four round apertures, provided with vibrating cilia. Their distribution is perfectly symmetrical, each pair lying upon the two opposite sides of the respiratory sac, one close behind the other and below their respective excretory apertures. Van Beneden (*l. c.* p. 44. pl. 3. fig. 11 *ff.*) has observed these apertures and discerned their true import.

The heart appears to be formed last of all. It represents at first, a very short sac lying on the right side, near the stomach, or rather near the abdominal furrow, distinguishable by its undulating but, at present, very slow movement. It is distended with blood-corpuscles, which are driven alternately hither and thither.

Before long the test gives way, over the three apertures of the body, whose margins have, in the meantime, become notched, and thus the young Ascidian enters into relation with the external world, since, from this time forth, it is enabled to take in nutritive matter and the water necessary for respiration. Before this, however, the second layer of the body on each side, in the entire neighbourhood occupied by the two apertures of the gills, has become detached from the respiratory sac, which elsewhere lies in close apposition with it, in the form of an externally convex roof. This roof therefore includes a cavity, which communicates on the one hand, by means of the respiratory apertures with the branchial sac, on the other by means of the corresponding excretory apertures, which are seated upon the summit of the roof, with the exterior; the terminal portion of the intestine, which has in the meanwhile become longer, curves at this time round the bottom of the respiratory sac upwards, and opens in the end, by means of the anus into the left space above mentioned*. In this way it becomes possible that the water drawn in through the anterior aperture of the body into the respiratory sac, should pass through the branchial apertures into the two spaces, and become emptied out again through the excretory apertures, whilst

* We shall subsequently recur once more to these two spaces.

the undigested remains of the food merely pass into the left space and are extruded through its aperture.

We soon see clearly that the heart pulsates more swiftly, and in addition in alternately opposite directions, and that the blood, which already had begun to oscillate in various parts of the body, now follows a determinate, though very simple course; this consists of a dorsal and an abdominal current, united by two transverse currents on each side, the one of which may be seen round the anterior aperture of the body, the other within the bridge formed by the wall of the respiratory sac between the two respective branchial apertures.

As regards the test, it has already been stated that the green aggregated vesicles originally deposited in it become afterwards changed into its granules; this change commences only subsequently to metamorphosis, and consists in the green structures gradually losing their cellularity and becoming smaller, less coloured, and more angular, and so by degrees assuming their ultimate form. It is only at a later period that those large, rounded, thin-walled cell-spaces appear, which, as is well known, occupy, closely appressed, the substance of the mantle in the full-grown animal (comp. Kölliker, *l. c.*). At first their number is but small, but afterwards they multiply, increasing in size at the same time, so that in this way the finer structure of the mantle becomes more and more perfect*.

In accordance with my plan I will now treat only of those organs whose further development is either interesting in itself, or has not yet been sufficiently investigated, and upon whose structure the study of development is calculated to throw some light.

We may consider, first, the respiratory sac, concerning the minute structure of which, in the adult animal, the following points may be called to mind. It is well known that its inner surface is divided into rectangular compartments by longitudinal and transverse ridges, which intersect one another at right angles. It is, besides, beset with numerous ciliated papillæ, one of which

* It is remarkable that the same metamorphosis of the green structures occurs also in the test investing the tail, which has been left behind as an empty sheath.

is placed at every crossing point of the ridges; the bottom of each compartment is pierced by from four to six narrow longitudinal clefts, the branchial apertures (*stigmates branchiaux*, Milne-Edwards), around whose edges is a fringe of numerous vibratile cilia. The bridges between these clefts are hollow, and receive the blood requiring aëration, brought to them on one side by the ridges, which are also hollowed, and carried away, on the other, after it has undergone the necessary change, to be redistributed by other ridges. The play of the cilia round the edges of the clefts drives the fresh water, continually drawn into the branchial sac, past the bridges.

As we know, however, the apertures lead into a large internal space (*chambre thoracique et cloaque*, Milne-Edwards) between the respiratory sac and the second layer of the body, which opens externally by the excretory or so-called anal siphon.

Of all those parts which contribute to the complicated organization of the respiratory sac, the most important, that is, the gill-clefts and the intervening bridges, are formed first; for we have seen the apertures appearing in the very earliest stages of development, as two rounded openings on each side. It was stated also that a current of blood was already established in the bridges. For a long time the respiratory sac possesses only these two pairs of apertures, which in the meantime elongate and become more and more cleft-like. At last there appear two new apertures on each side in the bridge between them, and soon afterwards another is added behind the originally posterior cleft, so that there are now altogether five openings. In this manner, successively and in serial order, a multitude of openings soon rapidly appear and pierce the two sides of the respiratory sac. At first, a second series is formed close to and above the first, then above this, a third and so more and more series, until the middle line of the back is reached. In similar succession rows of apertures appear, one below the other, between the first series and the abdominal surface. Like the original openings, all these appear, originally, as small gaps beset with vibratile cilia, and during their gradual enlargement undergo similar alterations in form, becoming more and more lengthened into clefts. It is easily comprehended that with the progressive increase of the respiratory sac, the number of the clefts also subsequently increases in

each series, and that new series continually appear between the old ones.

Soon after the respiratory sac has become thus perforated in its whole extent, we find the clefts, which previously had their long diameters disposed transversely to the axis of the branchial sac, arranged as in the adult animal with their long axes longitudinal. Many of the papillæ, covered with vibrating cilia, have at the same time become developed, upon the inner surface of the transverse and longitudinal bridges, between the clefts. The blood streams rapidly and abundantly through all the bridges. I have been unable to trace the development of the respiratory sac any further. In its present, by no means complete, structure, however, it singularly resembles the respiratory sac of the compound Ascidians. In this case we have again an example of the often enunciated and repeatedly confirmed law, that the higher forms of any given order of animals, at least as respects particular organs, exhibit transitorily, relations of form and structure which occur permanently, that is, in the adult state of the lower forms.

It will be recollected, that the three apertures of the body which were at first covered by the test, had opened externally after the appearance of the first gill-clefts and of the heart, in consequence of which the young Ascidian was enabled to take in nutritive matters and the water required for respiration. These apertures now become prolonged into short projecting tubes, the siphons. The aperture of the respiratory siphon, which from the beginning surpasses the two posterior or excretory siphons in circumference, soon appears fringed by eight lobes, as in the adult animal. In all the siphons the circular fibres, by whose action they are occasionally closed, may now be very readily distinguished under the test. Externally, above the circular bundles, there appear also a few longitudinally fibrous bundles, processes of the muscular bundles which, already interlaced, are disposed over the second layer of the body.

The ultimate fate of the two posterior siphons is particularly interesting, since, after persisting for a long time, they fuse together into the single siphon present in the adult. In fact, during the period in which the rapid multiplication of the respiratory apertures in the branchial sac is taking place, we see

the two siphons gradually approximate towards the middle line of the dorsal surface and at last come so close, that they are separated only by a small bridge. When the respiratory sac is completely perforated, this also disappears. Instead of the previous two excretory siphons, we now find a single one situated exactly in the middle of the dorsal surface, close behind the nervous ganglion; its lip is already, as in the adult animal, provided with six lobes.

The presence of two excretory siphons, at an earlier period, need not be at all surprising, if we recollect what has been previously stated respecting the two spaces which were formed over the original gill-clefts; it appears, in fact, to be almost a necessary consequence. It was shown that the two spaces are developed by the raising up of the second layer of the body, in the region of the apertures, from the respiratory sac, which is elsewhere closely applied to it. This mutual separation goes on to a greater and greater extent, during the further development of new clefts in the respiratory sac. The consequence is, that the boundaries of the two spaces extend further and further until at last, when the branchial sac is everywhere perforated, they coalesce upon the dorsal side, and in this manner constitute that inner space, between the branchial sac and the second layer of the body, to which we have already referred in the adult animal. When this has taken place there is no longer any need of more than one siphon, and, in fact, the formation of the single siphon is contemporaneous with that of the space in question.

I pass now to an organ, which in all the *Phallusiæ* surrounds the whole nutritive canal, from the mouth to the anus, and has the appearance of a compact honey-yellow mass, dotted over with chalky-white points. By the majority of zoologists, among whom we find a great authority (V. Siebold, *Vergleichende Anatomie*, p. 269), this structure has been regarded as a liver; a view which, to me, appears so much the more doubtful, as an organ which will subsequently be described, and which has hitherto escaped notice, probably has a greater right to this title. The organ now in question consists of obvious, clear, round, tolerably dense walled vesicles, the supposed simple glandular utricles in which the bile is prepared.

Every vesicle is apparently distended by a transparent fluid,

in the centre of which a solid concretion, in the form of a nucleus, may be remarked. In the larger vesicles the white chalky nucleus appears to be composed of two other rounded segments in close apposition, in the smaller it is perfectly spherical*. According to my observations the vesicles are all completely unconnected with one another; sometimes I thought I could make out a finely reticulated network upon the wall of some of them, without being able to come to any clear conclusion upon the matter. It is the more difficult to decide upon the purpose of the whole structure, as its mode of development, as we shall see immediately, does not throw the desired light upon it. One is tempted to consider it as a purifying organ, a kidney, which would agree very well with the deposits in the vesicles †. In that case, however, we ought to be able to discover excretory ducts, of which I could find not the least trace.

The first indication of this organ appears when the residue of the tail of the larva, reduced to a very few lobes, is rapidly disappearing. Close to these lobes, we see first a small, round, transparent vesicle, already precisely similar in structure to those of the adult organ. The round chalk-white nucleus is already visible in its centre. The vesicle now grows more and more, and at last, when the residue of the tail disappears, it takes its place close to the œsophagus on the left side. Subsequently a second vesicle is formed close to the first, after this a third, and so more and more, until the whole posterior space of the body between the œsophagus, the stomach, and the intestine, is filled up by a mass of such isolated vesicles, in every stage of development. Afterwards vesicles are seen arising singly and remote from the great mass near certain parts of the alimentary canal. In a few vesicles the nucleus appears double, in others it is provided with the previously mentioned mass of laminated crystals. Whether the vesicles arise at the same time with the nuclei, as we have here described it, or whether the nuclei, as would seem

* In *Phallusia monachus* the round nuclei exhibit a close concentric striation, which seems to indicate a deposition in layers. In many vesicles a mass of laminated or acicular crystals lies upon the nucleus; sometimes one vesicle or another contains, instead of the nucleus, a great prismatic crystal with pyramidally pointed ends.

† Delle Chiaje (*Animali invertebrati d. Sicilia citeriore*, t. iii.), to whom these concretions were not unknown, appears to hint at this interpretation.

o be theoretically more probable, are deposited from the fluid of the vesicles at a subsequent period, must be left undecided. I have but rarely seen the nucleus wanting at the first appearance of the vesicles. The organ could be traced no further in its development, which is, however, clear enough from what has just been stated.

Finally, it only remains that I should describe an organ as yet unknown, which is so hidden, as only to be partially visible in the full-grown animal. It consists of a system of fine canals, which are distributed over the whole intestine, commencing in cæcal extremities, which are partly cylindrical, partly, and for the most part, enlarged or clavate, and often locally sacculated; these enter into manifold anastomoses with one another, and thus enclose the wall of the intestine with a close network; at last they unite into twigs and branches. The canals are found, most abundantly, within the strong projection which runs along the inner surface of the intestine from the stomach almost to the anus, and which is besides filled with the vesicles of the organ which has been already described. The ramification of the branches and twigs, which frequently, during their course, perform arched curvatures somewhat in the manner of the vasa vorticosa of the eye, and in some places dilate into ampullæ, is dichotomous; the contents of the cæca and canals are pellucid. So much for the relations of this organ in the adult animal; development affords us the following further information.

Very early, even before the appearance of the first gill-clefts and of the heart, there appears at the beginning of the intestine immediately behind the stomach, a cylindrical process, altogether homogeneous, and with a somewhat enlarged, clavate, free extremity, which passes transversely, on the left side, to the vicinity of the terminal portion of the intestine. Without perceptible alteration, this process continues slowly to grow, until at last we see it divide at its extremity into many branches, which pass to and embrace the intestine.

Very soon these branches also divide, dichotomously, into twigs, which by their frequent anastomosis form a network enclosing the intestine. In this manner the ramification proceeds, the network upon the intestine becomes closer, and at last the cæca above referred to make their appearance upon it. The branches

now exhibit their characteristically wavy course, and in some places the ampulliform expansions. It is worthy of being remarked further, that at this time, when the organ, in fact, is but sketched out in its first rudiments, the main trunk of the canals, *i. e.* the original process, as well as its branches, are still homogeneous solid cords, whilst in the cæca and the twigs which have anastomosed into networks, the wall and the cavity are already distinguishable.

It results hence, that the organ which consists of branched canals opens by means of an excretory duct into the intestine, as an appendage of which it at first appears. Its whole structure would lead one to consider it to be a gland, whose secretion, prepared in the cæca, would seem, if we may judge by the place of insertion of the duct into the gland, to be accessory to digestion. Whether the watery secretion is bile and the gland therefore is a liver, must for the present be left undecided.

EXPLANATION OF PLATE XII. B.

Fig. 1. Embryo in a late stage. Two pigment spots already exist. *a*, body; *b*, commencement of the tail; *c*, *c*, the two upper processes of attachment of the larva commencing their development; *d*, anterior pigment spot; *e*, posterior pigment spot.

Fig. 2. Larva lying upon its side. *a*, *a*, test with the imbedded and as yet unchanged green structures; *b*, *b*, axis of the tail; *c*, *c*, hollow canal of the axis; *d*, the fin-like horizontal appendage into which the test covering the tail becomes expanded; *e*, anterior pigment spot; *f*, posterior pigment spot; *g*, upper right process of attachment; *h*, lower process of attachment.

Fig. 3. A developing *Phallusia* of the stage when the three apertures of the body have become already elongated into very short siphons. *a*, respiratory siphon wide open; *b*, *b*, the two posterior or excretory siphons in their contracted state; *c*, nervous ganglion with four nervous trunks; *d*, œsophagus; *e*, stomach; *f*, intestine (its terminal portion curves round the bottom of the respiratory sac upwards towards the left excretory siphon); *g*, coil of the larval tail breaking up into lobes and disappearing; *h*, *h*, *h*, *h*, the four first gill-apertures with their intermediate bridges; *i*, the dark, apparently single mass of pigment under the ganglion; *k*, abdominal furrow; *l*, *l*, test.

[J. H. H.]

ARTICLE XI.

Observations on the Development of the Pectinibranchiata.

By MM. KOREN and DANIELSSEN.

[From the *Annales des Sciences Naturelles*, t. xviii. No. 5, and t. xix.]

§ 1. *On the Development of* Buccinum undatum, *Linn.*

ALTHOUGH, since we first made known our investigations into the development of the Mollusca, in the *Magazin for Naturvidenskaberne*, many remarkable memoirs have appeared upon the same subject (those of Nordmann*, of Vogt†, of Quatrefages‡, of Lovèn §, of Reid ||, and of Leydig ¶), yet we think it advisable to set forth our observations here in full, and we trust that they will not be read without interest—particularly as we have been able, in two genera of Gasteropods, to follow step by step the development of the embryo from its first appearance to its complete formation, and as we shall have to bring forward facts new to science.

On the 1st of March, 1851, we procured many oviparous capsules of *Buccinum undatum*. It is well known that these capsules, spherical or ovoid in form, are most usually found united into racemes nearly as large as the fist. They are attached to various bodies, such as rocks, bits of old wood, marine plants, &c. In many of these racemes, the capsules contained incomplete young, in others ova. We possessed then all the materials required for our researches. To judge from the internal condition

* *Versuch einer Monographie von* Tergipes Edwardsii.

† *Recherches sur l'Embryogénie de l'Action* (*Annales des Sciences Naturelles*, 3rd ser. t. vi. 1846, p. 1).

‡ *Annales des Sciences Naturelles*, 3rd sér. t. iv. p. 33.

§ *Bitrag til Kœnnedomen om Utvecklingen af Mollusca Acephala lamellibranchiata* (*Kongl. Vet. Akad. Handl.* 1848).

|| *Ueber die Entwickelung der Eier der Mollusca nudibranchiata* (*Froriep's Jahresberichte*, Januar 1850).

¶ *Ueber* Paludina vivipara (*Zeitschrift für wissenschaftliche Zoologie*. Leipzig, 1850).

of the ova and from other evidence which we have obtained, it would appear that *Buccinum undatum* lays its eggs from the beginning of January to the end of April.

Many oviparous capsules were opened, and their contents subjected to microscopical examination. Each capsule enclosed a limpid pellucid viscous liquid, resembling white of egg; in this viscous humour and at the bottom of the capsule there lay a large number of ova (6–800), which could with difficulty be detached from one another; each egg was composed of a delicate transparent membrane (chorion), in the interior of which was another, still more delicate, enveloping the yelk. The latter, spherical in shape, was composed of a viscous fluid, in which was dispersed a multitude of rounded granules, variable in size and of a clear yellow colour (Pl. X. fig. 2). No trace of either germinal vesicle or germinal spot was visible; the diameter of the ovum varied between 0·257 and 0·264 of a millimetre.

On the 8th, 13th, 15th and 20th of March we re-examined capsules of all the racemes; the ova had remained, to our great astonishment, spherical and without division*.

On the 24th of March the ova were still undivided, but instead of being scattered as before, they had approximated to one another. The chorion had begun to disappear; the larger portion of the yelk was diffused (*s'était épanchée*), and invested by the viscous albuminous fluid which surrounded the vitelline membrane. Some days afterwards, the ova had become agglomerated into a single mass, which at its surface was divided into many portions, in which each ovum could be distinguished by the naked eye. In general the number of the ova constituting each of these portions varied from six to sixteen.

On the 29th of March again, we examined many capsules; the isolated groups were more sharply defined and each mass had become ovoid or reniform; it was observable also that these groups were united together.

On the 1st of April we examined many capsules; one of them enclosed twelve embryos; they were ovoid or reniform, and provided with two rounded lobes (vela) and a foot (figs. 3. 4 *c* & 5 *e*.). The fluid contained in this capsule was as clear as

* We have at times, in a few ova, seen a small conical eminence upon the vitellus.

water and perfectly fluid, so that the embryos could easily be extracted from it. In another capsule there were but six embryos, four of which were well formed.

We began then to form a conception of the import of all these facts; but they seemed to us to be so extraordinary, that for a long time we did not venture to put confidence in our observations—so different were these results from all that had hitherto been seen with respect to the development of Mollusks, and even from all known physiological phænomena. But the attentive study of what went on under our eyes at last cleared away all our doubts, and led us to dispute a law generally admitted and based upon a great number of facts. In fact, we had before us a mode of development which required for its proper understanding much new investigation; and it appeared to us to be indispensable to follow out these singular phænomena in neighbouring genera, in order to see if, towards the limits of this zoological group, we should find them disappearing; an anticipation which, as we shall see by and by, has been fully justified.

But let us first trace out these phænomena in the *Buccinum*, and we shall find them surprising enough; for we shall look in vain in a fecundated ovum, for any of those changes which in ordinary cases take place during its development, in virtue of the well-known law of yelk-division. We see no grooving—no cell appears; in a word, the interior of the ovum remains without alteration; on the other hand, external to it we observe active alteration. The excessively viscous albuminous fluid collects and, so to speak, glues together the ova, which were primarily separate, uniting them into bunches; subsequently the mass in which they were immersed, from being viscous, becomes as liquid as water; and it is then that we first perceive traces of activity in the ovum itself. Its external membrane bursts in certain places—the yelk becomes diffused, and a membrane, destined to circumscribe the developing individual, is produced around each bunch of ova; between these bunches we see many isolated ova, which seem excluded from this organic process which gives rise to embryos. We do not know if these isolated ova die at once, or undergo a further imperfect development; but in any case they are beings, whose existence is but ephemeral. As soon as the grouped ova are invested by their

membrane, the formation of the embryo begins; a very clear, finely granular and viscous liquid is deposited at first on the external surface of the ovum. In this plastic mass we see, in some localities, cells developed, in others muscular tubules, according to the nature of the organ which is to be produced; thus, the first signs of activity visible about the ova, after they are laid, are observed in the very viscous albuminous mucus which surrounds them, and this activity is manifested by the mere union of a certain number of ova into more intimate relations. We imagined at first, that these phænomena of agglomeration might represent yelk-division; but we soon gave up this idea, which seems to us altogether incorrect*. Besides, the development of *Purpura lapillus*, which we have subsequently examined, and in which division and the phænomena of agglomeration go on at the same time, has also contributed to our rejection of this notion. We come therefore to the conclusion, that yelk-division is not always indispensable for the production of the embryo; but the fact of the agglomeration of some fifty or more perfectly formed ova, into a single individual, is certainly strange enough. Where does the formative principle exist? Is it enclosed in an isolated ovum? Or is it extended over the whole mass? and is it the common power which becomes then the organizing force of the substance? We have seen the isolated ova undergoing a certain amount of development, but the being which results from them is very incomplete and becomes very rapidly destroyed. It would seem to want the materials requisite for its permanent existence. We shall return to this subject in treating of the development of *Purpura lapillus*, and we shall confine ourselves here to adding, that this

* In publishing here the observations of MM. Koren and Danielssen, which are highly interesting in themselves, apart from the interpretation which may be put upon them, we consider ourselves bound to remark, that the rounded masses of vitelline matter, regarded by these authors to be simple ova, seem to us to be merely vitelline spheres, whose utriculiform envelope presents a little more consistence than ordinarily, and that therefore the aggregation from whence the body of the embryo arises, is the result of the grouping together of the vitelline spheres of a single ovum, and not the product of the union of many primitively distinct ova. What these authors remark with respect to the phænomena of yelk-division, which are also sometimes observed in these spheres, would in nowise oppose this interpretation.—(*Note by* M. Milne-Edwards.)

mode of development appears to us to be of great physiological importance and will assuredly be confirmed by further observations. With regard to the number of ova which are grouped together for the formation of a single embryo, there is considerable variation, and it seemed to us to be the greater, the greater the number of the ova in the same capsule. In the mean, each capsule contains from six to sixteen embryos; however, we have found as many as thirty-six. The more ova there are in a capsule, the more of them there are in each mass, whence we sometimes meet with embryos which have at their first appearance a very considerable size,—attaining in fact as much as $1\frac{1}{2}$ millimetre. The number of ova united into one embryo varies from 40 to 60; we have often, however, met with as many as about 130.

Gray long since observed*, that a capsule enclosing more than a hundred ova yielded only four or five embryos. The English physiologist explains this fact by the law of atrophy, that is to say, by supposing that the great increase of some ova hinders the development and ultimately effects the destruction of the others. It remains to be seen whether Gray deceived himself, or whether it is we who have fallen into error. We believe that he was on the right track, but did not attain to the exact truth.

After having seen that the ova group themselves together, to form the embryo, and become coated by a delicate and transparent pellicle, we now proceed to explain the manner in which the various organs make their appearance. The first step is the exudation of a clear, finely granular substance over the surface of the ova, which then begin to appear more transparent. We perceive in this mass, a multitude of cells which continually multiply; it then takes on a distinct form and becomes bilobed (fig. 4 *c*). These lobes are gradually provided with cilia, and the first movements are exhibited. The foot, which is formed in a corresponding manner, appears as an eminence, distinct from the remainder of the body, and presenting cilia; the embryo then turns upon itself in an extremely slow manner (fig. 5 *e*). Scattered cirrhi† now make their ap-

* *Annales des Sciences Naturelles*, 2 Sér. tom. vii. p. 375.

† Sars drew a distinction between the long cirrhi which are found on the lobes and the cilia, and proposes to call them *natatory hairs* (Svœmmehaar). Subsequently many authors have called them *cirrhi*, retaining the name of *cilia* for the very short, fine hairs.

pearance here and there upon the upper edges of the rounded lobes, and in a short time spread over their whole surface (figs. 5 & 6); the lobes are then rounded and provided with cilia, as well as with cirrhi (fig. 15). After the formation of the lobes and of the foot, we see a semi-transparent granular substance between the grouped ova and the membrane which invests them, exuding and becoming the rudiment of the mantle, covering itself superficially with a membrane which occupies a greater or less space and takes on a determinate structure (fig. 4). Subsequently we observe, on the lowest part of the mantle, a hemispherical transparent body, which is the rudiment of the shell (figs. 5, 6, 7*a*). The foot increases in size and takes on a more rounded form, and at its base we distinguish early the two auditory organs (figs. 7, 8, 9*g*). They are constituted by two spherical vesicles, pellucid as water, filled with a perfectly transparent and colourless liquid, and early exhibiting a double contour. Each vesicle encloses but a single otolith. When the animal is placed under the compressorium these organs become very distinct, and by increasing the pressure, each otolith readily becomes separated into four regular segments. The vibratory movement which most authors have observed in these otoliths, has not been observed by us in those of *Buccinum undatum*, neither have we been able to distinguish any cilia upon the internal surface of the vesicle, although we have employed the strongest magnifying powers.

The eyes probably appear at the same time as the auditory organs, for we have never seen the latter without being able to observe the former. Leydig has remarked, that the rudimentary eye is a vesicle which exists at the root of the tentacles. We have confirmed the exactness of this observation; the internal surface of this vesicle is always provided with cilia (fig. 10*a*). It is filled with a liquid, enclosing a quantity of pigment-granules, of a strong, clear yellow colour, which are invested by an excessively fine pellicle (fig. 10*b*). At this period the vibrating cilia communicate a rotatory movement to these granules. We have been unable to distinguish any lens at this period; it is only subsequently developed. At the same epoch as that in which the eyes appear, we also found the two conical tentacles and the rudiments of the salivary glands; the latter always make

their appearance as two pyriform organs, composed of rounded cells (figs. 8 & 9 *h*); their lower extremity is the thicker, and their centre is filled by a mass of deeply coloured pigment-granules. The keel-shaped heart appears at the same time, as well as the mouth and the rudiments of the proboscis. Sars, Lovèn, Nordmann and Vogt have been unable to discover any heart in the first periods of development, and we have ourselves sought it in vain in many Nudibranchiate genera; we are therefore led to conclude that the first period of development passes by without the existence of this organ. It is not the same with the Pectinibranchiata, at least with *Buccinum undatum* and *Purpura lapillus*. In these the heart has already appeared in the interval between the twenty-third and the twenty-eighth day. Grant* was the first to observe the heart in *Buccinum undatum*, and to draw attention to its strong pulsations. To the same observer we owe the discovery of the two rounded organs provided with vibratile cirrhi upon the sides of the head, by the aid of which the embryos move about in *Purpura*, *Trochus*, *Nerita*, *Doris*, and *Eolis*. Subsequently, Lund, Sars, Lovèn, Nordmann and other naturalists, have confirmed the exactness of these observations. The heart lies upon the dorsal side, a little to the left, is a little twisted and completely uncovered at its first appearance; for different organs which cover it afterwards, such as the roof of the branchial cavity, are still rudimentary. In the place where the heart is about to appear, a grayish, transparent, finely granular mass, having a rounded form, arises; it is attached to the lobes and the foot, and presents no sensible movement. Soon, slight contractions are perceptible; the form becomes more and more marked, and at last it resembles a great clear vesicle. Two or three muscular tubes, of extreme delicacy, are now traceable upon its parietes and effect its contractions. In this primitive state, the heart possesses the form which it will subsequently retain (fig. 6 *e*). In proportion as its parietes increase in thickness and magnitude, the muscular tubes are multiplied, transverse tubes appearing and becoming filled with a transparent and colourless liquid (figs. 7, 8 & 9 *e*); we have often counted the pulsations, and have found that their rate varies; on the average, there were some forty to

* Edinburgh Philosophical Journal, 1827, vol. vii. p. 121.

fifty a minute; they are not always regular and frequently change their character; strong pulsations occur among the weaker pulsations. It frequently happens that the heart suddenly ceases to contract, remaining at rest for some time; and it is nowise uncommon to observe strong pulsations succeeding intervals of rest. The cavity of the primitive heart is cylindrical, and is divided by a single partition. Its parietes are excessively delicate, very transparent, and refract light in an altogether different manner from the other organs (fig. 8 *e*); we have never met with any liquid nor with any cellular structure in them. We have also observed similar muscular tubes in the two rounded lobes*; but here we see that many are superimposed and frequently ramify. This branching becomes more and more abundant as we approach the periphery of the lobes, where the finer ramifications frequently interlace and a muscular network results (fig. 15 *a*,*b*) which serves to move the two rounded lobes in all directions. It may be, that a vascular network exists in some parts of this muscular reticulation, for little granules, refracting the light strongly, are to be met with dispersed through the mass. Since the two distinguished French naturalists, MM. Milne-Edwards and Valenciennes, have pointed out the greater or less incompleteness of the vascular system of Mollusks, it has appeared to us to be important to observe the condition of the circulation in the young *Buccinum*, but notwithstanding all our efforts, we have not been sufficiently fortunate to detect the slightest trace of a circulating current†.

We have already stated that the proboscis is one of the organs that appears early; it is recognizable by its cylindrical form and

* Leydig, *l. c.*, describes the structure of the muscles of a great number of Gasteropoda, and remarks that the result of his researches upon this subject does not altogether agree with that at which MM. Lebert and Robin have arrived. We believe that those of Leydig are the more exact in all essential points, inasmuch as they agree better with our own observations.

† We cannot help remarking that there is something very anomalous about this supposed "heart," and we would venture to suggest that its structure and position indicate rather, that it is no heart at all, but a "contractile vesicle," similar to that which exists in the corresponding locality in the pulmonate Gasteropoda, and which, acting in concert with the caudal vesicle, performs the functions of a heart before the true heart makes its appearance. See Gegenbaur, *Beiträge zur Entwickelungsgeschichte der Land Gasteropoden*, Siebold und Kölliker's *Zeitschrift*, 1852. [T. H. H.]

by the strong muscular contractions which it presents. A little later, the stomach and the œsophagus appear; the latter presents itself under the form of a hollow cylinder attached to the proboscis, and presenting upon its parietes, which are of excessive thinness, a certain number of clear striæ, the rudiments of the future muscular tubes. As soon as the œsophagus becomes free from the proboscis, it bends a little backwards and upwards, running along the lower surface of this organ for a short distance; then, having undergone a flexion in the opposite direction, it directs itself a little to the left to terminate in the slightly elongated portion of the stomach (fig. 12 *n*). It is extremely difficult to follow the early phases of the development of the œsophagus; for it is surrounded by the proboscis, whose parietes are both thicker and more opake than its own; in some places it is entirely covered by it. It is for this reason, that we have been unable to determine if the œsophagus is formed, at once, in all its length, or if a portion appears at first, and elongates until it becomes united with the stomach. The latter organ is found a little to the left, and, at first, is almost spherical. It appears to arise thus: a grayish semitransparent mass exudes from a single yelk, soon becoming invested by a delicate pellicle, which completely encloses this same yelk (fig. 9 *m*). This membrane at first stretches upwards to become united with the œsophagus, and afterwards downwards to give rise to the intestine, which turns towards the right side of the body (fig. 11 *o*). It is by reason of this origin that we see the stomach always filled, so to speak, with yelk-granules, which are constantly agitated by the vibrating cilia with which the parietes of the stomach are provided. These cilia are found, not only on the internal surface of the latter organ, but we have also observed them in the œsophagus and in some parts of the intestine. As we have been unable to follow the intestine for more than a small portion of its course (fig. 11 *e*), we have not made out the anus.

It is at this period that the first outlines of the nervous system are distinguishable: they are two compact, ovoid and yellow bodies (cerebroid ganglia), which surround the œsophagus; and about the same time, the rudiments of the two pedal ganglia, placed side by side, having a strong yellow hue and more or less ovoid in form, make their appearance.

After the edges of the mantle have developed themselves into a covering over the back of the animal, a cavity clothed with fine cilia is formed, in which the heart and branchiæ lie. The first traces of branchiæ which we observed were two indistinctly marked bands arising from the edge of the mantle, and diverging at intervals to unite again and so form loops. We have found, at a more advanced stage, that these bands are tubes taking a very sinuous course, whence they have a certain resemblance to a corkscrew. These sinuosities were better marked above and below than in the middle, where they were wider and more closely appressed; an active ciliary motion was distinguishable upon their internal edge (11 *p*). Lovèn has shown, in his excellent memoir (*op. cit.*), that there is an extreme resemblance, in respect of development, between the Gasteropoda and Acephala; he has described the mode of formation of the branchiæ in the latter, and we have observed even that the production of these organs takes place in a similar manner in *Buccinum undatum* and *Purpura lapillus*.

About the period of the formation of the branchiæ we observed, below, at their union, a vesicle which is formed and developed like the heart. It is ovoid or slightly pyriform, ends below in a very long tube which follows the course of the intestinal canal, and eventually, like the latter, becomes lost in the obscure mass of the yelk (11, 12 *q*). Its walls are thin, semi-transparent, and provided with a multitude of varicose muscular tubes which take a direction both longitudinal and transverse to the vesicle. These tubes have smaller dimensions than those of the heart, and for that reason it is necessary, in order to distinguish them readily with the microscope, to employ a much higher power than that required to examine the muscles of the heart.

The contractions of the bladder are strong, and take place from above downwards, whilst the heart contracts from one side to the other.

When this vesicle dilates it becomes filled with a clear liquid in which a great number of obscure molecules are distinguishable. We can regard this organ as nothing but the kidneys.

The period for the development of new organs has now gone by, but all those already formed, become gradually perfected.

The head and the back of the animal are now distinct, and are provided with fine cilia and with much elongated tentacles, resembling cilia. The eyes are more conical, and their lenses are distinctly perceptible. The buccal aperture appears in the form of a transverse cleft. The proboscis is perfectly developed. The tongue appears in it with its armature such as Lebert and Lovèn have described. The salivary glands are very voluminous, and their excretory canals may be readily traced passing along the sides of the œsophagus. The siphon is already much developed, and provided with cilia (fig. 13 *g*). The form of the foot is modified, being considerably elongated; in addition, two rounded lobes have arisen in its upper part; its surface is ciliated all over (11,12*f*). As regards its structure, the foot is composed of a multitude of primitive muscular tubules—some cylindrical, others varicose—running in all directions, without however uniting into bundles. We have never been able to detect either granules or cells in these tubes.

At this period the nervous system has become very distinct. We see that the two ganglia placed at the sides of the œsophagus (cerebroid ganglia, 11*t*,12*p*,14*f*) are united by a commissure; from each of these ganglia a very thick commissure passes (12*q*, 14*i*) to unite them to the pedal ganglia (12*r*, 14*k*), which are ovoid, with their small extremities turned towards the cerebroid ganglia, and furnish a great number of branches for the foot, (fig. 14 *l*.)

We see besides, in the lobes of the foot, two smaller, also ovoid ganglia (12*s*,14*m*) which send branches to the lobes. Two commissures (14*m*), unite them to the pedal ganglia: the cerebroid ganglia distribute a nervous twig to each eye and to each auditory organ (14*g*&*h*). We have observed that one of the pedal ganglia sends a nerve to the intestinal mass (fig. 14*p*).

The description given by Cuvier of the nervous system of this mollusk* differs in many points from what our observations have shown us. It is certain, that the nervous mass which Cuvier has called the cerebrum is a pedal ganglion; for we have seen, in the adult animal, that the true cerebroid ganglion which surrounds the œsophagus, and which, without doubt, escaped his notice, is situated above this latter ganglion.

* *Mémoires pour servir à l'Histoire de l'Anatomie des Mollusques.* Paris, 1817

The shell, which is membranous during the first periods of the development of the embryo, excessively delicate and ovate or reniform, subsequently takes on the form of that of the Nautilus (fig. 11 *a*), but subsequently becomes,—by degrees, more ovoid. The calcareous particles then begin to be deposited in considerable numbers, forming very obvious longitudinal and transverse striæ, and the shell is much less transparent than before. However, it is still possible to distinguish the internal organs: the heart and the bladder have divided into two chambers, the upper of which is the smaller. When the auricle contracts, the ventricle dilates, and *vice versâ*. A very strong muscle is also observable, arising from the internal surface of the shell and passing to the foot (fig. 11 *s*); its office is to retract the animal into its shell. Finally, the liver appears upon the under surface of the stomach; it is ovoid, and is formed of a mass of granules containing yellow pigment (fig. 11 *r*). On the inner surface of the mantle a series of folds may be observed (*feuillets muqueux*, Cuvier), in which lie a mass of mucous crypts.

Subsequently the little animal continues to grow; more and more calcareous particles are deposited in the shell: the mantle thickens, and it becomes almost impossible to distinguish the internal organs. The two rounded lobes have disappeared, but behind the tentacles we see a linear eminence indicating the place they occupied. The shell has assumed a horn-yellow colour; it becomes hard, brittle, and only semitransparent. It was commonly in this state that the young left its capsule, after a residence of at least eight weeks there, creeping around the vessel in which it had been kept, with tentacles, foot, and siphon protruded. The little whelks are now distinguishable from the adults, only by their shell having not more than one or two spiral turns. We may add, that we have found no traces of generative organs in these young. The ova, grouped together in considerable numbers, occupy the posterior part of the shell.

§ 2. *Purpura lapillus*.

The ovigerous capsules are not unlike a little flask whose rounded end is directed upwards—and its delicate neck, by the extremity of which it is attached to stones or other bodies, downwards (Pl. XI. fig. 1). Each capsule is hermetically closed, and

contains a transparent, pellucid, viscous liquid, like the white of egg—investing a mass of ova (60 or more).

A number of the ova were placed under the microscope, after freeing them from the viscous humour in which they had been enclosed, and we saw that they possessed a delicate chorion, a vitelline membrane, and a yelk consisting of a liquid, with many contained granules. We were unable to distinguish either germinal vesicle or spot. Each ovum was 0·194 millim. in diameter.

After some days had elapsed, we opened another capsule, and observed, in the greater number of ova, the commencement of a cleavage which appeared to be altogether irregular. In fact, the number of spheres indicated by this cleavage was very variable; and some of the ova, which, we may add, were all provided with a chorion, had assumed an ovoid form (figs. 3, 4, 5, 6, 7, 8, 9). The cleavage masses were all dark, and unprovided with any nucleus.

M. Nordmann has been equally unable to observe any nucleus in *Tergipes*, *Rissoa*, or *Littorina*. The clear body which MM. Van Beneden, Nordmann, H. Rathke, F. Müller, Lovèn, and other authors, have seen passing from the interior of the vitellus to its surface (to which F. Müller and Lovèn attribute the power of determining the cleavage), has not appeared in the ova we are describing, although we have taken great pains to look for it*.

Some days later we examined many other capsules. The viscous albuminous humour had undergone no appreciable change. However, the ova were not so scattered as before, and had approached one another. Examining them microscopically, we observed that some had undergone no division; others had remained in a state of incipient division,—while around these imperfectly developed ova there were a great number of others in which division was more advanced. We see then, in this case, that the ova have a disposition to collect together, and that although enclosed in the same capsule, they exhibited a great difference in the extent to which the cleavage process had taken

* In a very recently published Appendix to this Memoir (*Supplement til Pectinibranchiernes Udviklings-historie*, af J. Koren og D. C. Danielssen), the authors give an account of new observations on this point in *Buccinum undatum*. In examining the youngest ova they have seen the clear (oily) body pass out, and they describe, at length, the mode in which this takes place.

place. In these ova, 2, 4, 6, 7, 9, 10, and even 18, cleavage masses might be counted; the contents of all were obscure, and without any nucleus. Even at this period, we thought we noticed a tendency to agglomerate the ova in the viscous liquid, analogous to that whose effect we observed in *Buccinum undatum*, but it was far from being well marked, and the commencing cleavage threw great obscurity upon what was going on. But all our doubts were completely dissipated on the twelfth day, when the phænomenon which had been exhibited by *Buccinum undatum* was repeated by *Purpura lapillus*. In fact, the ova were agglomerated and formed a compact mass; the viscous and albuminous liquid had at the same time become as clear as water, and could be separated from the conglomerate with great ease. Examining the latter with attention we observed that it was composed of many groups of various extent and without any determinate form; these groups, under the microscope, appeared to be composed of ova, the greater number of which had undergone cleavage, while others had not (Pl. XI. fig. 24).

On the sixteenth day we re-examined many capsules. All the ova were agglomerated, but the conglomerate was a little altered, inasmuch as certain groups had become more distinct, more sharply circumscribed, and projected more from the common mass. Some were cylindrical, others pyriform, but they were all terminated by a peduncle which connected them with the common mass (fig. 27). The microscopical examination of each group showed it to be formed by the union of ova imbedded in a very viscid mass, and invested by a delicate membrane, which soon became covered with very fine cilia (fig. 27). The ova themselves had undergone no further cleavage, and it appeared to us that this process had stopped as soon as the agglomeration commenced. Soon after, we observed a well-marked grayish, semitransparent, finely granular matter, exuding from the sides of the above-mentioned peduncle, and becoming, at a later period, covered with vibratile cilia (the foot) (figs. 26, 27 & 28 *b*). We also observed a similar mass becoming developed, in the same manner, at the base of the peduncle, and giving origin to two lobes, which afterwards increased and acquired fine cilia at their edges (fig. 7 *d*). The embryo thus constituted now begins to move a little by the help of its cilia. In fact, it was observed to make feeble efforts in various directions, as if it

sought to detach itself from the common mass—and having, at length, after many fruitless attempts, succeeded in so doing, it immediately began to rotate upon itself. We have, in this manner, observed all the individuals of a conglomerate, becoming detached and separated, one after the other, and when all the embryos were developed, the mass had totally disappeared. It would seem that in this animal, as in the *Buccinum*, the number of ova which are grouped together to form the future embryo is altogether variable and fortuitous, for not only is there no discoverable law regulating their union, but these conglomerates are constituted by very different numbers of ova. Thus we have observed in the same capsule some embryos resulting from the union of three or four ova, while sixty or more, had contributed to form most of the others. The different size of the individuals depended on the same cause. This difference of size was very considerable, for we observed swimming in the liquid contained in the capsule, some embryos of $\frac{1}{4}$ millim. in diameter, and others of as much as $1\frac{1}{3}$ millim. The number of the embryos in a given capsule varied as much as their size;—depending in the same manner on the greater or less number of the ova which had united to form each individual. On the average we found from twenty to forty, rarely more.

Having now become acquainted with the mode of formation of the embryo in *Purpura lapillus*, let us turn to another phænomenon, one of the most surprising which is to be met with in the development of this mollusk, and which will help to explain the singularity in the development of *Buccinum*, to which we have already referred. It will be remembered that in the latter animal, many of the ova took no share in the act of conglomeration (probably in consequence of accidental obstacles), and that their ova soon died, or rather became developed in an excessively incomplete manner. Something similar occurs in *Purpura*; and as we have had better opportunities for observing this peculiarity in the latter mollusk, we are enabled to give a fuller account of it. We have always found in each capsule an ovum undergoing all stages of cleavage, and which was composed, until the end, of a peripheral layer of clear, and a central mass of dark cells (figs. 10 & 11). A membrane then became rapidly developed around the yelk, and acquired exceedingly fine cilia; at the upper part of the peripheral layer there were also visible

the rudiments of the two rounded lobes (velum) with the foot (figs. 12 *a*, *b*, *c*. 13 & 14 *b*, *c*). Cilia quickly made their appearance both on the foot and on the lobes: subsequently, scattered cirrhi could be observed upon the lobes, and then the embryo began to rotate. Later still the lobes and the foot increased in size (figs. 15, 16 *b*, *c*), and the rudiments of the auditory organs (fig. 16 *d*) appeared at their base,—the membranes of the mantle became more and more thickened, the shell began to be formed on its most sloping part, and calcareous particles to be deposited in it (figs. 14, 15, 16 *a*). The embryos whose first development we have just been following were true monsters, and subsequently assumed such various and whimsical forms, that no one could have imagined them to be individuals of the same species. In a few we have seen the salivary gland appear (fig. 16 *e*), but it was the only new structure which appeared after the formation of the external organs, and these beings permanently remained in the same state of arrest of development. Finally, until eight weeks had elapsed, this monstrous embryo was always to be met with in the capsule. We have already stated that an ovum of this nature always existed in each capsule, and its embryo was known at once by its small size and the excessive vivacity of its motions. We have sought for them in vain in the capsule after eight weeks, and we suppose that they had all perished. When our attention was first directed to these simple ova, which had regularly undergone the cleavage process, we imagined that their development had taken place in a normal manner; but, far from this, it was, in fact, an abortion. For the viability of the individual organized, more than one ovum is necessary: and despite the regularity and the vivacity observable in the young product of the single ovum, we see that its development remains in the highest degree incomplete. This single ovum had in fact undergone all the stages of cleavage, and to all appearance united all the anatomical and physiological conditions necessary to its complete development,—while, on the other hand, it appears to us to be incontestable, that it had never been in possession of the materials requisite for the formation of organs. Without doubt there is much that is obscure in these ideas; we shall endeavour by and by to throw as much light as we can upon them.

Having described the monstrous embryo resulting from a

single ovum, we may return to the embryos formed by multiple ova, and describe at length their further development.

We have already remarked, that after the formation of the ciliary membrane, the foot and the two rounded lobes are the organs first developed. At about the same time we perceive a transparent mass between the membranes and the conglomerate ova (fig. 28 *d*). Cells are developed in this mass in layers, and give rise to the mantle (figs. 29, 30*b*). The most sloping part of the latter secretes a very clear and viscid humour, which increases by degrees and forms the rudiment of the shell, which, when it first appears, resembles a clear and gelatinous pellicle, wherein subsequently calcareous particles are deposited (fig. 29 *a*). These particles afterwards increase in number and impede the examination of embryos which are a little older.

The lobes are small at first, but their volume rapidly increases; a multitude of cilia appear on the surface, cirrhi are developed from their upper edge and produce much more vivacious movements (figs. 29 *d*, 30 *e*). The foot becomes strongly separated on the ventral surface and thus forms a transverse eminence (fig. 28 *b*), which rapidly increases in volume and exhibits the first rudiments of the auditory organs at its base, developed as in *Buccinum undatum* (figs. 29 *e*, 30*f*). At the same time as the auditory organs, the rudiments of the tentacles, of the eyes and of the salivary gland, appear. The tentacles commence as two conical eminences, at the base of which the eyes are visible as two rounded vesicles, filled internally with a pellucid liquid; dark pigment granules may be seen in them (fig. 31 *l*, *m*). We have been unable, at this stage of development, to discover any lens, nor have we met with any cilia on the internal parietes of the vesicle.

The first trace of the salivary glands which manifests itself, is a mass of rounded cells upon each side of the base of the foot, which are usually nucleated. These cells soon acquire a delicate membrane, which afterwards elongates to meet the future œsophagus, whose outlines are not yet distinguishable. In proportion as the salivary glands are developed, these cells become more and more multiplied in their interior and are closely disposed in elongated lines; we see also, in the widest portion of this organ, a mass of dark yellow pigment granules. In its more

delicate part, directed towards the œsophagus, the excretory duct of the gland is indicated, and elongates to meet this portion of the intestinal canal (Pl. XI. figs. 30, 31 *g*, Pl. XII. fig. 4). The salivary gland forms but a single conglomerate mass in the adult, but its double excretory duct shows clearly enough, that it was divided into two parts in the very youngest state.

The heart was seen on the twenty-third day. The mode of its development is analogous to that which occurs in *Buccinum*. It is situated upon the dorsal side, presents the form of a bladder, and is directed from above downwards and from left to right; it contracted in this direction, at the rate of forty to fifty pulsations a minute. It possesses primitive muscular fibres, having the form of longitudinal tubes, undivided above. We have met with neither cells nor nuclei in these tubes (Pl. XII. figs. 1, 3 *h*).

In this stage of development, the branchial cavity is not deep enough to contain the whole of the heart, a considerable portion of which extends beyond the edge of the mantle. Subsequently, when the mantle elongates and covers in the back of the animal, its edge is directed more outwards and detaches itself from the body, so that the branchial cavity becomes deeper and wider and encloses the heart completely.

We have as yet been unable to observe the circulatory current in this mollusk.

It is only after the formation of these organs that the buccal aperture, the proboscis and the œsophagus, are perceptible. The proboscis is exceedingly short and its parietes are very thick, so that it is easily seen through the œsophagus (fig. 31 *i*). The latter is cylindrical and takes a course beneath the stomach (figs. 31, 32 *k*). The latter lies to the left, it is small and oval, and a long and delicate intestine passes out of it, which turns to the right, bends back afterwards to the opposite side in a curved direction, and finally terminates in the branchial cavity by a projecting anus (fig. 32 *l*, *m*, *n*).

The œsophagus, the stomach and the intestine are ciliated upon their inner surface.

It is not until a somewhat later stage of development that the nervous system is distinctly discoverable. It is composed of two cerebroid ganglia upon each side of the œsophagus (figs. 31 *n*,

32 *q*); these ganglia are united by means of a commissure, and give rise to two other commissures (fig. 31 *n*, *s*), which connect them with the pedal ganglia. They are oval, are distinguished by their clear yellow colour, and send a great number of branches to the foot (fig. 32 *s*).

We have been unable to trace the nervous system further, all parts of the body having rapidly become opake. It is also about the time of the appearance of the nervous system, that the first traces of the branchiæ, of the siphon and of the retractor muscles of the foot, are discoverable. The branchiæ spring from the edge of the mantle and then form a hollow cylinder, which is twisted into loops; fine cilia appear upon its inner edge. Subsequently it becomes a little flattened and considerably spread out. In its parietes, longitudinal and transverse fibres are discoverable, which we regard as muscular tubules. The cilia which exist in the middle of each loop have an extraordinary length (Pl. XII. fig. 8 *b*, *c*).

After the development of the branchiæ, it becomes exceedingly difficult to make out the formation of the other organs; on the one hand, because the animal rarely protrudes from the shell sufficiently to show these parts, and on the other, because the mantle is greatly thickened and a large quantity of calcareous matter has been deposited in the shell. The latter has taken the shape of that of a Nautilus, and when it is placed under a strong magnifying power, it is observable that the calcareous matter is deposited in the form of a network with fine meshes (fig. 2). The two rounded lobes diminish in volume (fig. 5). The foot, lobed above, takes on more and more the shape of that of the adult animal, and the operculum which closes the aperture of the shell is completely developed (fig. 6). The heart is, in this stage, divided into two chambers, whence the great vessels arise. The lenses of the eyes are clearly distinguishable, and we have frequently met with a single eye presenting two streaks of pigment, but never with more than one lens. The branchial cavity, whose internal surface is covered with cilia, has become, at this period of development, deep enough to enclose the heart completely. The edge of the mantle, which divaricates further and further from the body of the animal, is ciliated, and at the bottom of the branchial cavity

we observe, for the first time, a contractile vesicle similar to that which exists in *Buccinum undatum*.

After the lapse of eight weeks the young had not yet left the capsule, but when one was taken out, it began to creep like the adult animal, with foot, tentacles and siphon stretched out. It is then distinguished from the adult by the incomplete disappearance of the lobes, by the shell being still soft, and by the spire having only one or two turns (fig. 6). From the ninth and tenth weeks the young begin to leave the capsules, the rounded lobes disappear, and behind the tentacles an elevated line may be seen occupying their previous place (fig. 7); the shell has elongated and approximates more nearly that of the adult; it is hard, frangible, and almost opake; the last turn of the spire, however, is not yet formed.

We shall not describe the development of the organs of *Purpura* at greater length, because it does not differ from what we see in *Buccinum undatum*.

We may call the attention of the reader to the interesting investigations of Kölliker and Siebold* on *Actinophrys Sol* and on *Diplozoon paradoxum*; for, perhaps, something approximating to what we have just described may be found in their observations.

In conclusion, we may add, that we entertain a strong desire to have the opportunity of continuing our investigations upon other genera allied to *Buccinum* and *Purpura*, for assuredly, with some slight modifications, all these Mollusks are developed in the same way.

Summary.

For the more ready comprehension of the history of the development of *Buccinum undatum* and of *Purpura lapillus*, we here shortly sketch the most essential points.

Buccinum undatum.

1. The ovigerous capsule is filled with a transparent, colourless viscous liquid which resembles white of egg. Each capsule encloses a mass of ova (of 6–8 centimetres).

* *Zeitschrift für wiss. Zoologie*, tom. i. p. 198, and tom. iii. p. 62.

2. Each ovum consists of a chorion and albumen, of a vitellary membrane, and of a vitellus composed of larger or smaller globules. Its diameter varies from 0·257–0·264 millim. In the egg, when laid, we have never been able to observe either germinal vesicle or spot.

3. The cleavage which occurs in other mollusks does not take place in these animals.

4. The ova begin to approximate towards the eighteenth day, and the chorion is detached. The yelk, more or less laid bare, invested only by its very firm membrane, is enveloped by the viscous albumen-like liquid.

5. Some days later, the ova, even those which were most distant, approximate and form only a single mass, whose different portions, larger or smaller, have become grouped; so that each group, usually composed of from six to sixteen ova, is distinguishable by the naked eye.

6. On the twenty-third day, these groups are still more distinctly marked out, and are invested by a very delicate membrane peculiar to each group, which has by this time taken on an oval or reniform shape: the ova are connected together, and the liquid which enclosed them has lost its viscosity.

7. Towards the twenty-fifth day the groups possess a more decided membrane and boundaries. Many of the ova which have remained isolated and simple appear as embryos, whilst the others are attached together.

8. The embryo thus formed consists of a delicate membrane enclosing many ova.

9. The number of the ova grouped to form one embryo varies greatly, amounting in some cases to as many as a hundred and more.

10. The number of embryos in different capsules varies; commonly it is from six to sixteen.

11. The first organs which are formed after the membrane in question are the rounded lobes with cilia and cirrhi. [The embryo then begins to move.] At a later period, the foot, the mantle, the shell, the auditory organs, the proboscis, the eyes, the salivary gland, the heart, and the contractile bladder appear; still later, the digestive and the nervous systems and the branchiæ, are developed.

12. After an interval of at least eight weeks, we see the young leave their capsule; the shell is a little more elongated (about 2 millim. long), hard, frangible and semitransparent. The lobes have disappeared, and the young animal creeps like the adult; it is still distinguishable by the number of the turns of its spire (there are only one or two). We should observe, that we have hitherto found no traces of the generative organs in these young.

13. Finally, the grouped ova are sufficiently numerous to fill the posterior part of the shell.

Purpura lapillus.

1. The ova, dispersed through an extraordinarily thick and viscous humour, fill the ovigerous capsules of the animal, which are flask-shaped.

2. The size of the ovum is about 0·194 millim. This ovum is composed of a delicate chorion, of an albumen, of a vitelline membrane and yelk.

3. The vitellus undergoes a very irregular cleavage. The cleavage masses have no nuclei.

4. After a certain progress of the cleavage, the ova begin to be grouped together.

5. On the twelfth and thirteenth days the ova have become, so to say, a compact mass, subdivided into many masses of ova, disposed in bunches.

6. On the sixteenth day the separate groups were more sharply circumscribed, and projected from the remainder of the mass. These projecting groups soon took a cylindrical or pyriform shape, and were fixed to the rest by means of a peduncle. The microscope showed them to be composed of a delicate ciliated membrane, and that they enclosed a mass of ova; a transparent substance exuded from the two sides of the peduncle, upon which fine cilia appeared (the foot); and at the base of this same peduncle the first traces of the lobes were distinguishable. Finally, many of these pyriform bodies became detached from the mass and rotated upon themselves; these were the embryos.

7. It is impossible to determine the exact number of the ova which go to form one embryo, as it varies greatly. In each capsule

an embryo proceeding from a single ovum is constantly met with; but this embryo never attains to a complete development.

8. The number and size of the embryos vary in different capsules; the average number is from 20–40. The largest embryo was $1\frac{1}{4}$ millim. in diameter.

9. The first organs which are formed after the tegumentary membrane are the foot with its vibratile cilia and the two rounded lobes, which are both ciliated and provided with cirrhi; then the mantle, the shell and the auditory organs, the salivary glands, the heart (on the twenty-third day), the eyes and the tentacles. The digestive apparatus, the nervous system, the branchiæ, the siphon, and the retractor muscles of the foot, appeared later still. Subsequently the heart divides into two chambers, the shell presents one or two spiral turns, and it is only after all these changes that the contractile bladder appears.

After eight weeks the young had not yet left the capsules; and when one was extracted in this stage of development, it began to creep like the adult animal, from which however it was distinguished by the lobes, which had not wholly disappeared, and by the shell, which still had only one or two spiral turns.

10. Towards the ninth or tenth week, the young leaves the capsule; the lobes have disappeared; the shell has become fragile and opake.

EXPLANATION OF THE PLATES.

Buccinum undatum. Plate X.

Fig. 1. An egg from the oviduct of *Buccinum*, × 200. *a*, yelk; *b*, germinal vesicle; *c*, germinal spot.

Fig. 2. Egg from a capsule, × 200. *a*, chorion; *b*, vitellary membrane; *c*, yelk.

Figs. 3 & 4. Embryos. *a*, chorion; *b*, yelk with its membrane; *c*, rudiments of the two lobes.

Fig. 5. Embryo seen from the side. *a*, membranous shell; *b*, mantle; *c*, yelk; *d*, lobes; *e*, foot.

Fig. 6. Embryo. Dorsal view. *e*, heart.

Fig. 7. Embryo. Ventral view. *f*, foot.

Fig. 8. Embryo. Dorsal view. *h*, salivary glands.

Fig. 9. Embryo. Ventral view. *i*, tentacles; *k*, proboscis; *l*, œsophagus; *m*, stomach.

Fig. 10. Embryo from the side. *a–g*, as in the foregoing figures; *h*, eyes; *i*, tentacles; *k*, proboscis.

Fig. 11. Young *Buccinum* seen laterally. *a*, shell; *b*, mantle; *d*, lobes; *e*, heart; *f*, foot; *g*, auditory organ; *h*, operculum; *i*, head; *k*, eyes; *l*, tentacles; *m*, mouth; *n*, stomach; *o*, intestine; *p*, branchiæ; *q*, bladder; *r*, liver; *s*, muscles; *t*, cerebral ganglia; *u*, commissures; *v*, pedal ganglia; *x*, commissure; *y*, ganglia of the pedal lobes.

Fig. 12. Young seen laterally. The same letters as in the foregoing figures, except *o*, salivary glands; *p*, cerebral ganglia; *q*, commissure; *r*, pedal ganglia, with their nerves; *s*, ganglia of the pedal lobe; *t*, commissure; *u*, siphon; *v*, branchiæ.

Fig. 13. Dorsal view of young. *a*, shell; *b*, mantle; *c*, foot; *d*, head; *e*, eyes; *f*, tentacles; *g*, siphon.

Fig. 14. Nervous system of a young individual seen laterally and compressed. *a*, head; *b*, eyes; *c*, tentacles; *d*, foot; *e*, œsophagus; *f*, cerebral ganglia; *g*, optic nerve; *h*, auditory nerve; *i*, commissure; *k*, pedal ganglia; *l*, nerves of the foot; *m*, commissure; *n*, ganglion of the pedal lobes; *o*, its nervous branches; *p*, intestinal nerve.

Fig. 15. One of the lobes, × 400. *a*, primitive longitudinal tubes; *b*, transverse simple tubes; *c*, calcareous granules; *d*, cilia; *e*, cirrhi.

Fig. 16. Eyes of an embryo, × 400. *a*, capsules whose external and internal surfaces are ciliated; *b*, membrane enclosing pigment granules.

Purpura lapillus. Plate XI.

Fig. 1. Ovigerous capsule, containing ova in different states and of the natural size.

Fig. 2. An egg magnified. *a*, chorion; *b*, vitelline membrane; *c*, yelk.

Figs. 3, 4, 5, 6, 7, 8. Ova, in various stages of cleavage, magnified.

Fig. 9. Embryo magnified. *a*, ciliated membrane; *b*, cells.

Fig. 10. Embryo many days older. *a*, ciliated membrane; *b*, peripheral cells; *c*, central cells.

Fig. 10 *b*. The same, × 350.

Fig. 11. An embryo at nearly the same stage of development.

Fig. 12. A rather more advanced embryo, viewed laterally. *a*, membrane, *b*, the two lobes; *c*, the rudimentary foot.

Fig. 13. An embryo, viewed laterally, × 350. *a*, shell; *b*, lobes; *c*, foot.

Fig. 14. An embryo, viewed laterally, × 350. *a*, shell; *b*, lobe; *c*, foot, *d*, mantle.

Fig. 15. An embryo, viewed dorsally, × 380. *a*, shell; *b*, lobes; *c*, foot; *d*, mantle.

Fig. 16. An embryo, × 350. *a*, shell, in which calcareous granules are deposited; *b*, lobes; *c*, foot; *d*, auditory organ; *e*, rudiments of the salivary gland; *f*, mantle.

Figs. 17, 18, 19, 20, 21, 22, 23. Ova in different stages of development.

Fig. 24. Grouped ova.

Fig. 25. Ovum, slightly magnified, and taken out of the capsule to show the result of the grouping. *a*, grouped ova, which have not yet taken a decided form; *b*, embryo in the earliest state.

Fig. 26. An embryo, strongly attached to the mass, × 100. *a*, membrane; *b*, foot; *c*, ova, grouped in various stages.

Fig. 27. Embryo, × 100. *a*, membrane, ciliated here and there; *b*, foot; *c*, peduncle; *d*, rudimentary lobe; *e*, grouped ova.

Fig. 28. Embryo, × 100. *a*, membrane; *b*, foot; *c*, lobe; *d*, exuded mass; *e*, grouped ova.

Fig. 29. Embryo, × 100. *a*, shell; *b*, mantle; *c*, foot; *d*, lobe; *e*, auditory organ; *f*, grouped ova.

Fig. 30. Embryo, viewed laterally, × 100. *a*, shell; *b*, mantle; *c*, grouped ova; *d*, foot; *e*, lobe; *f*, auditory organ; *g*, salivary gland; *h*, heart; *i*, rudimentary stomach.

Fig. 31. Embryo, viewed laterally, × 100. *a*, *b*, *c*, *d*, *e*, *f*, *g*, *h*, as in fig. 30; *i*, proboscis; *k*, œsophagus; *l*, tentacle; *m*, eyes; *n*, cerebroid ganglia.

Fig. 32. Embryo, viewed laterally, × 100. Letters as before, except *l*, stomach; *m*, intestine; *n*, anus; *o*, tentacles; *p*, eyes; *q*, cerebroid ganglia; *r*, commissure; *s*, pedal ganglia.

Plate XII.

Fig. 1. Heart, × about 450. *a*, auricle; *b*, ventricle; *c*, primitive muscular tubes; *d*, large vessel.

Fig. 2. Calcareous network, × about 450.

Fig. 3. Embryo at the twenty-third day.

Fig. 4. Salivary gland.

Figs. 5, 6, 7, 9. Embryos further advanced.

Fig. 8. Developing branchia.

THE END.

Fig. 1.

Fig. 3.

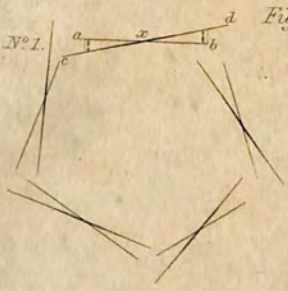
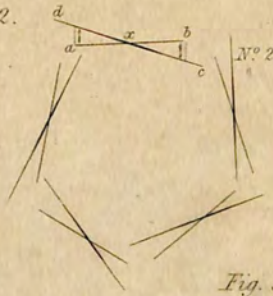


Fig. 2.



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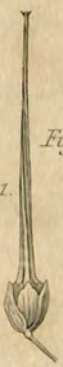


Fig. 4.

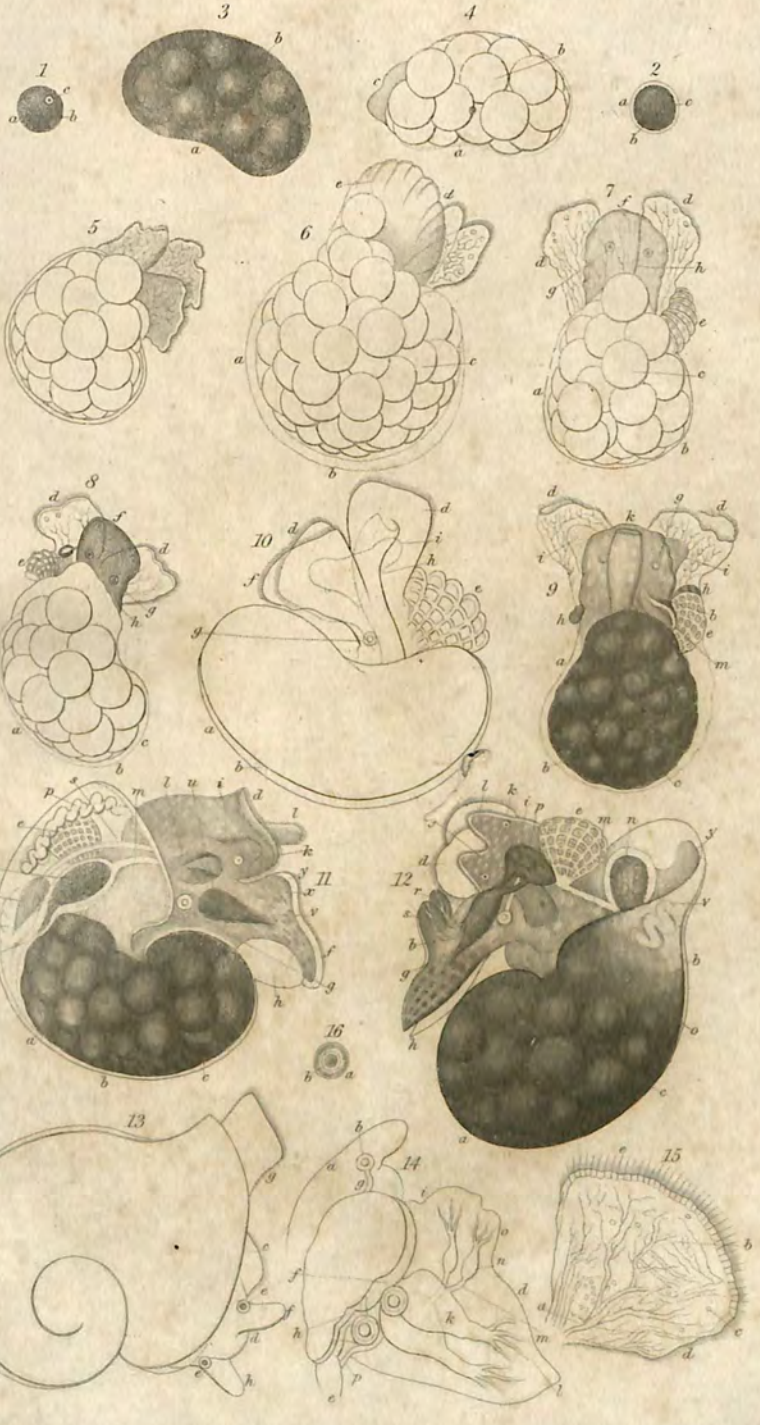
N°1.

N°2.

Fig. 6.

Fig. 7.

Fig. 9.



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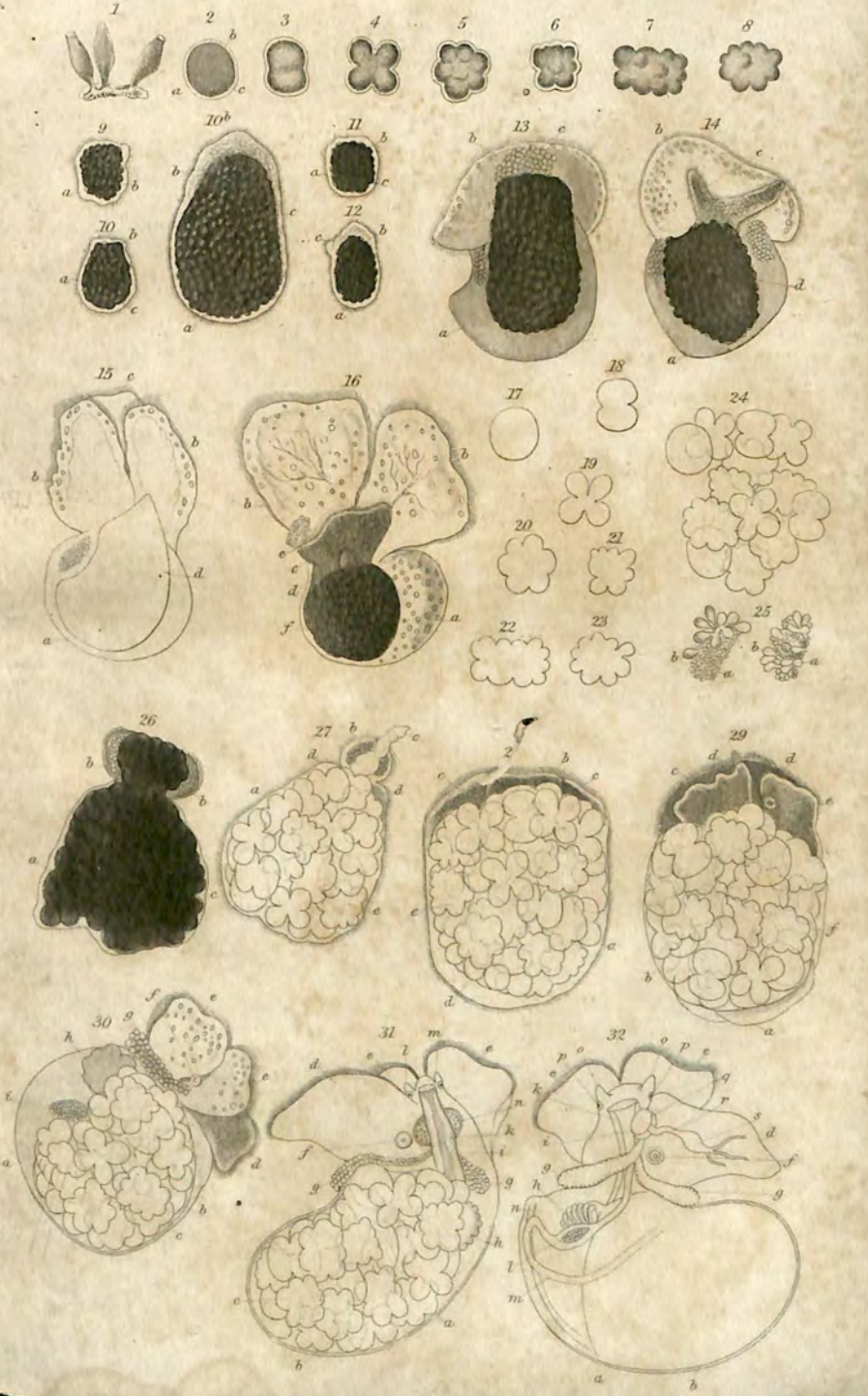
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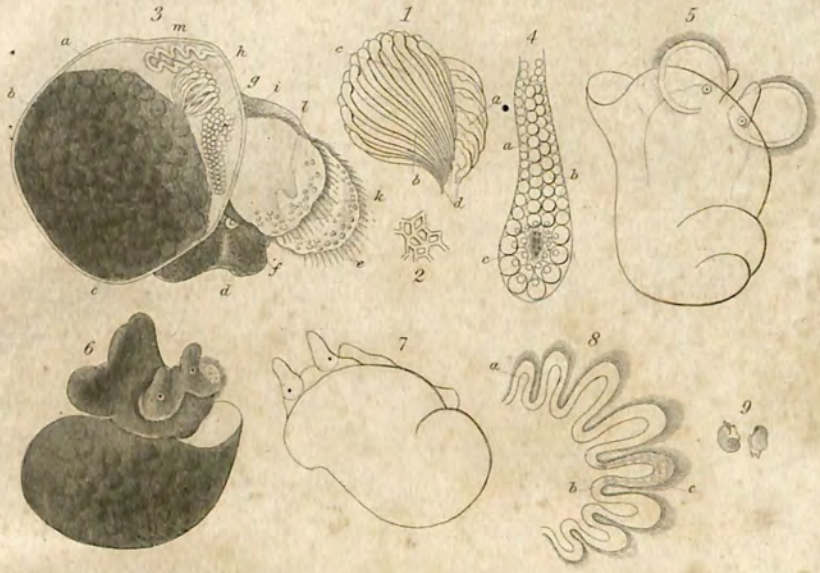

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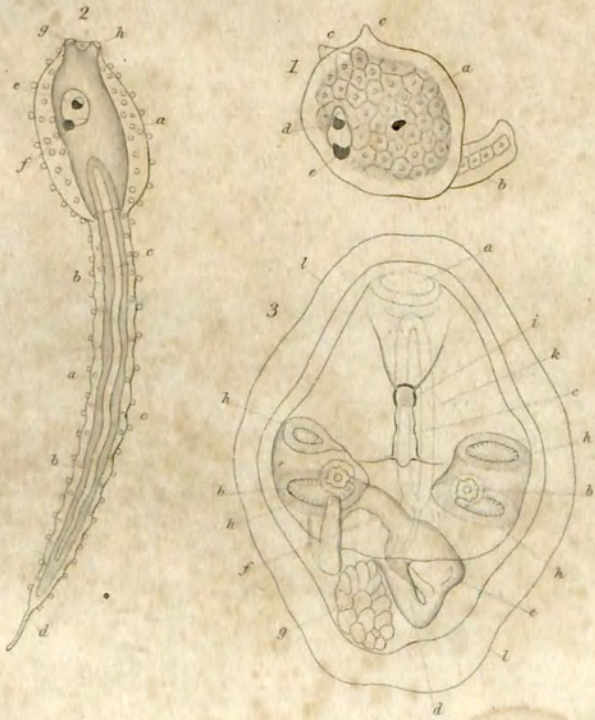

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